1	Batagur baska
2	Batagur borneoensis
3	Batagur dhongoka
4	**Batagur kachuga**
5	Batagur trivittata
6	Hardella thurjii
7	Malayemys
8	Morenia ocellata
9	Morenia petersi
10	Orlitia borneensis
11	Pangshura smithii
12	Pangshura tecta
13	Pangshura sylhetensi
14	Pangshura tentoria
15	Geoemyda japonica
16	Geoemyda spengleri
17	Siebenrockiella crassi
18	Cuora amboinensis
19	Cuora aurocapitata
20	Cuora flavomarginata
21	Cuora galbinifrons
22	Cuora mccordi
23	Cuora mouhotii
24	Cuora pani
25	Cuora trifasciata
26	Cuora yunnanensis
27	Cuora zhoui
28	Heosemys annandalii
29	Heosemys depressa
30	Heosemys grandis
31	Heosemys spinosa
32	Leucocephalon yuwor
33	Mauremys annamens
34	Mauremys caspica
35	Mauremys leprosa
36	Mauremys japonica
37	Mauremys mutica
38	Mauremys nigricans
39	Mauremys reevesii
40	Mauremys rivulata
41	Mauremys sinensis
42	Melanochelys tricarin
43	Melanochelys trijuga
44	Notochelys platynota
45	Sacalia bealei
46	Sacalia quadriocellata
47	Vijayachelys silvatica
48	Rhinoclemmys annula
49	Rhinoclemmys areola
50	Rhinoclemmys funere
51	Rhinoclemmys nasuta
52	Rhinoclemmys punctu
53	Rhinoclemmys rubida
54	Geoclemys hamiltonii
55	Gopherus polyphemu
56	Emydoidea blandingii
57	Clemmys guttata
58	Chrysemys picta
59	Rhinoclemmys diaden
60	Rhinoclemmys melan
61	Rhinoclemmys pulche
62	Batagur affinis
63	Cyclemys
64	Cuora picturata
65	Terrapene carolina
66	Stigmochelys pardalis
67	Malaclemys terrapin
68	Echmatemys septaria
69	Echmatemys wyominc
70	Bridgeremys pusilla
71	Guangdongemys ping
72	Isometremys lacuna
73	Mauremys thanhinen
74	Hardella siamensis
75	Sinohadrianus sichua
76	Sinohadrianus ezoen
77	Sharemys hemisphae
78	Palaeochelys elongat
79	testu

A new testudinoid turtle from the Middle to Late Eocene of Vietnam and its implication for geoemydid systematics (#30840)

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- ! Is it correctly described e.g. meets ICZN standard?

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2

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A new testudinoid turtle from the Middle to Late Eocene of Vietnam and its implication for geoemydid systematics

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Background. Testudinoidea is a major clade of turtles that has colonized different ecological environments across the globe throughout the Tertiary. Aquatic testudinoids have a particularly rich fossil record in the Tertiary of the northern hemisphere, but little is known about the evolutionary history of the group, as the phylogenetic relationships of most fossils have not been established with confidence, in part due to high levels of homoplasy and polymorphism. **Methods.** We here focus on describing a sample of 30 testudinoid shells, belonging to a single population that was collected from lake sediments from the Middle to Late Eocene (35–39Ma) Na Duong Formation in Vietnam. The phylogenetic placement of this new material is investigated by integrating it and 11 other species of putative geoemydids from the Eocene and Oligocene to a recently published matrix of geoemydid turtles, that embraces the use of polymorphic characters, and then running a total-evidence analysis. **Results.** The new material is highly polymorphic, but can be inferred with confidence to be a new taxon, *Banhxeochelys trani* gen. et sp. nov. It shares morphological similarities with other southeastern Asian testudinoids, *Isometremys lacuna* and *Guangdongemys pingi*, but is placed phylogenetically at the base of Pan-Testuguria when fossils are included in the analysis, or as a stem geoemydid when other fossils are deactivated from the matrix. The vast majority of other putative fossil geoemydids are placed at the base of Pan-Testuguria as well. **Discussion.** The phylogenetic placement of fossil testudinoids used in the analysis is discussed individually and each species compared to *Banhxeochelys trani* gen. et sp. nov. The high levels of polymorphism observed in the new taxon is discussed in terms of ontogenetic and random variability. This is the first time that a large sample of fossil testudinoids has its morphological variation described in detail.

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INTRODUCTION

Testudinoids are an ecologically diverse and speciose clade of turtles (Ernst & Barbour, 1989) that colonized many terrestrial and freshwater environments over the course of the Tertiary (e.g., Sukhanov, 2000; Lapparent de Broin, 2001; Danilov, 2005; Vlachos, 2018) and now have a near global distribution with 190 extant species (TTWG, 2017). Geoemydids, one of the four primary clades of Testudinoidea, have a particularly rich fossil record in the Paleogene of the northern hemisphere (e.g., Claude & Tong, 2004; Hervet, 2004a; Hutchinson, 2006; Vlachos, 2018), especially in freshwater environments. Notable forms from this time interval include the North American *Echmatemys* lineage (e.g., Hay, 1908; Vlachos, 2018) and the European *Palaeoemys* and *Ptychogaster* lineages (e.g., Danilov, 2005; Hervet, 2006). The Paleogene record is still rather poor for the group in Asia (Gilmore, 1931), but notable remains have recently been described from the Early Oligocene of Thailand (i.e., *Hardella siamensis* and *Mauremys thanhinensis*; Claude, Suteethorn & Tong, 2007) and the Late Eocene of China (i.e., *Guangdongemys pingi* and *Isometremys lacuna*; Claude et al., 2012).

Although some effort has recently been placed on resolving the morphology and taxonomy of Paleogene geoemydids (e.g., Hervet, 2004a; Hervet, 2004b; Claude & Tong, 2004; Claude, Suteethorn & Tong, 2007; Claude et al., 2012), little is still known about the evolutionary history of the group, as the phylogenetic relationships of most fossils have not been established with confidence (Claude et al., 2012). This is probably related to high levels of homoplasy and polymorphism found in geoemydids (and testudinoids, in general) that precludes the performance of traditional phylogenetic analysis (Joyce & Bell, 2004; Garbin, Ascarrunz & Joyce, 2018).

A sample of approximately 100 geoemydid skeletons, mostly incomplete shells, was recently collected from the Middle to Late Eocene Na Duong Formation as exposed at the Duong coal mine in Vietnam (Böhme et al., 2013). The purpose of this contribution is to describe this new geoemydid material, which is considered to represent a single, new species, and to assess its phylogenetic significance by placing it in a character taxon matrix that embraces polymorphic characters.

GEOLOGICAL SETTING~~S~~

The available sample of approximately 100 specimens was collected between 2009 and 2012 from the Na Duong Formation at the Na Duong coal mine, which is located in Loc Binh district, Lạng Sơn Province, Vietnam (Fig. 1). The Na Duong Formation is a 240 m thick continental deposit consisting of marly claystones, siltstones, and fine to medium-grained sandstones intercalated with lignite seams and extractable coal seams (Böhme et al., 2011, 2013). The vast majority of vertebrate finds made at this locality originate from a single horizon at the base of the main lignite seam (layer 80 of Böhme et al., 2011). Based on sedimentology, mineralogy, fauna and flora the lignitic shales of layer 80 are interpreted as representing a shallow acidic lake deposit (Böhme et al., 2013). Testudinoids are by far the most abundant vertebrates from this horizon. The same horizon has otherwise yielded trionychid turtles, cyprinid and amiid fishes, three species of crocodiles, and anthracothere and rhinocerotid mammals (Böhme et al., 2013). As all testudinoid specimens described herein were collected from about 50 cm of the same stratigraphic horizon, they are thought to represent a true population. The magnetostratigraphy in combination with the anthracotherid and rhinocerotid mammals suggest a late Middle to Late

Eocene age (i.e., upper Bartonian – late Priabonian) for the Na Duong formation. For a more detailed discussion, please refer to Böhme et al. (2013).

NOMENCLATURAL ACTS

The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The Zoobank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSID for this publication is urn:lsid:zoobank.org:pub:D2620202–9814–4F81–BFA4–043EB1B6F948. The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central and CLOCKSS.

SYSTEMATIC PALEONTOLOGY

TESTUDINES Batsch, 1788

CRYPTODIRA Cope, 1868

TESTUDINOIDEA Fitzinger, 1826

PAN-TESTUGURIA Joyce, Parham & Gauthier, 2004

***Banhxeochelys trani* gen. et sp. nov.**

Holotype. GPIT/RE/09760, a nearly complete shell lacking left peripherals VII–XI, left costals VII and VIII, the pygal, part of right peripherals VI and VII, and a part of the left xiphiplastron.

Type locality and horizon. Na Duong coal mine, Long Binh District, Lạng Sơn Province, Vietnam; base of the main lignite seam (layer 80 of Böhme et al., 2013), upper Bartonian–late Priabonian (34–39Ma), late Middle to Late Eocene (Böhme et al., 2013).

Etymology. "Bánh xèo" is a dish from Vietnam that resembles a crepe or pancake. "Chelys" derived from the Greek, meaning turtle. The genus name is formed in allusion to the highly compressed, pancake-like preservation of the type material. The species name honours Đặng Ngọc Trần, retired director of the International Cooperation Division of the Department of Geology and Minerals of Vietnam, for his untiring support of the excavations carried out by teams from the University of Tübingen from 2009 to 2012.

Diagnosis. *Banhxeochelys trani* gen. et sp. nov. can be diagnosed as a representative of Testudinoidea by the presence of a contact between plastral and marginal scutes and the corresponding absence of inframarginal scutes II and III, as a representative of Pan-Testuguria by the presence of a pygal bone that is wider than long, as a representative of Testuguria by the presence of short anal scutes, and as a representative of Pan-Geoemydidae by the presence of anterior musk duct foramina (*mdf*; Fig. 2), complete intersection of the pygal bone by the intersulcus of marginals XII (Figs. 3 and 4), a median keel on the carapace, and a cervical scute (Figs. 2, 3 and 5).

The following combination of characters is unique to this taxon: neural IV octagonal, neural V square, the remaining neurals hexagonal with anterior short-sides, two lateral keels on the carapace in juveniles (Fig. 2), entoplastron intersected anteriorly by gularohumeral sulcus (Figs.

2 and 3) and posteriorly by humeropectoral sulcus (Figs. 3 and 5), and short epiplastral lip in visceral view (Fig. 6).

Referred material. GPIT/RE/09749 (Fig. 6), subadult, incomplete carapace and epiplastra; GPIT/RE/09731 (Fig. 7), adult, complete carapace and plastron; GPIT/RE/09732 (Fig. 8), adult, incomplete carapace and plastron; GPIT/RE/09733 (Fig. 5), adult, complete carapace and plastron; GPIT/RE/09739, juvenile, incomplete carapace and plastron (rear part missing); GPIT/RE/09750, juvenile, incomplete carapace and complete plastron; GPIT/RE/09751, adult, complete carapace and incomplete plastron; GPIT/RE/09752, adult, epiplastra, entoplastron, hyoplastra, and incomplete carapace; GPIT/RE/09753, subadult, complete carapace and plastron; GPIT/RE/09754, adult, almost complete carapace and plastron; GPIT/RE/09736, adult, incomplete plastron; GPIT/RE/09755, adult, incomplete carapace and plastron; GPIT/RE/09748, subadult, incomplete carapace and plastron; GPIT/RE/09741, juvenile, incomplete carapace and plastron; GPIT/RE/09756, adult, incomplete carapace and plastron (xiphiplastra missing); GPIT/RE/09742, juvenile, incomplete carapace and plastron (xiphiplastra missing); GPIT/RE/09757, subadult, almost complete carapace and plastron; GPIT/RE/09737, adult, incomplete carapace and plastron; GPIT/RE/09738 (Fig. 9), adult, almost complete and plastron; GPIT/RE/09758, adult, almost complete carapace and complete plastron; GPIT/RE/09759 (Fig. 10), juvenile, complete carapace and plastron; GPIT/RE/09760 (Fig. 2), subadult, almost complete carapace and plastron; GPIT/RE/09743 (Fig. 11), juvenile, almost complete carapace and plastron; GPIT/RE/09740, juvenile, incomplete carapace and plastron; GPIT/RE/09734, adult, incomplete carapace and almost complete plastron; GPIT/RE/09735 (Fig. 3), adult, almost complete carapace and complete plastron; GPIT/RE/09745, subadult, incomplete carapace and plastron; GPIT/RE/09746, subadult, incomplete carapace and plastron; GPIT/RE/09747 (Fig. 4), subadult, posterior rear of carapace, hypoplastra and xiphiplastra; GPIT/RE/09744, juvenile, incomplete carapace and plastron.

Measurements. see Table 1

DESCRIPTION

Preservation. The new turtle material from the Na Duong formation is characterized by strong dorsoventral compression caused by post-depositional deformation. This precludes making observations to the visceral sides of the carapace and the plastron in most specimens. The pattern of sulci that normally characterized the surface of turtles is furthermore missing in numerous specimens due to surficial weathering of the pyritized shells. Not a single individual of the new turtle is therefore known by a complete specimen that preserve~~d~~ all scute sulci and bone sutures. Nevertheless, the 30 best preserved individuals used herein (14 adults, 8 subadults and 8 juveniles) in combination, provide information regarding the majority of shell structures and intraspecific variation.

Size Classes. To better understand the implications of the high morphological variation observed in our sample of *Ba. trani*, we separated the specimens into three maturity categories (i.e., adult, subadult and juvenile) according to the median length of hypoplastron trend in our sample (HypoML; Fig. 12). Specimens with a hypoplastron length around 40mm or less and presence of carapacial keels where classified as juveniles. Specimens with an average hypoML of 60mm, presence or not of carapacial keels where classified as subadults. And finally specimens with 70mm or more of hypoplastron median length where considered adults.

Carapace. A median keel is present in animals of all size classes, with exception of GPIT/RE/09732. Two lateral keels, on the other hand, are only present in smaller specimens, here interpreted as juveniles (Fig. 2). The median keel is low and continuous, anteroposteriorly directed, and crosses the entire neural series anteroposteriorly (e.g., Figs 2 and 10), starting over neural I or II and sometimes reaching to first suprapygal (Figs. 3 and 4). In GPIT/RE/09749, the median keel starts at the nuchal, on the anterior region of vertebral I. In most specimens, the median keel spans from vertebral I to V, but is restricted in GPIT/RE/09748 and GPIT/RE/09742 to vertebrals II and III. The lateral keels are located over the costals, are closer to the neurals than the peripherals, and either extend anteroposteriorly from pleural scutes I to IV (from the posterior region of costal I to the anterior region of costal VII) or are restricted to pleurals II and III (between costals III to VI). Growth annuli are evident on the carapace of some specimens (e.g., GPIT/RE/09743 and GPIT/RE/09745), but no size trend is apparent.

Nuchal. The nuchal resembles that of other pan-geoemydids by being hexagonal, the anterior margin being wider than posterior margin, and its maximum width being located around mid-length. The median keel emerges at the posterior half of the nuchal in GPIT/RE/09749 (Fig. 6). The ventral side of the nuchal is exposed only in GPIT/RE/09751, but it is not possible to see any characteristics due to bad preservation.

Neurals. Eight neurals are present, with exception of GPIT/RE/09738, which show nine neurals, probably due to an anomalous division of a neural VIII (Fig. 9). The neural bones vary in shape from anterior to posterior. Whereas neurals I to IV are longer than wide, neurals V to VIII are as wide as long or wider than long. Neural I is always squarish and either has rounded lateral margins that form an oval shape (in 57% of specimens), parallel lateral margins that form an overall rectangular shape (in 25% of specimens), or convergent lateral margins that form an triangular shape (in 18% of specimens). Neurals II to VIII are hexagonal with anterior short-sides, with the exception of neural IV, which is octagonal with short anterior and posterior sides, and of neural V, which is quadrangular or rounded. GPIT/RE/09759, a juvenile, and GPIT/RE/09748 are the only specimens that have hexagonal neurals with short anterior sides, including neurals IV and V. Usually all neurals are crossed anteroposteriorly by the median keel, with exception of GPIT/RE/09748 and GPIT/RE/09742 that have a median keel restricted to neurals III to VI.

Costals. Eight pairs of costal bones are present in the carapace, which do not alternate in length as in testudinids. Costal I is the anteroposteriorly longest element, about twice as long as costal II. While costals II to VI have about the same length and width, costals VII and VIII are significantly small in both dimensions. Costals VII and VIII never contact their counterpart at midline, as they are always separated by the neural series. A contact of the left axillary buttress with the visceral side of costal I can be observed in GPIT/RE/09751. No other specimens show clear evidence for axillary or inguinal buttress or their contacts with the costals. The lateral contacts of the costals with the peripherals are described below.

Peripherals. Due to the strong dorsoventral compression of the material, the peripherals are poorly preserved. In the majority of the specimens, the peripherals are displaced or shifted ventrally to partially cover the costals (e.g., GPIT/RE/09732; Fig. 8). Eleven pairs of peripherals are present. In general, the peripherals are not serrated, with exception of posterior peripherals of some specimens (e.g., Fig. 4). The lateral peripherals do not form a gutter. While peripheral I contacts the nuchal bone laterally, peripherals I–III contact costal I posteromedially. Peripheral IV contacts costal I and II and peripheral V contacts costals II and III medially. Peripheral VI contacts costal IV medially in GPIT/RE/09743, but costals IV and V in GPIT/RE/09759, the only two specimens where these contacts are visible. Peripheral VII contacts costals V and VI. Ventrally, peripherals IV to VI form the bridge by contacting the hyo- and hypoplastron. In

GPIT/RE/09743 it is possible to see the insertion of the axillary and inguinal buttresses at peripherals III and VII, respectively (Fig. 11). An anterior musk duct foramen can be observed on the ventral side of peripheral III in GPIT/RE/09751, GPIT/RE/09752, and GPIT/RE/09758. The posterior musk duct foramen, on the other hand, is visible on the ventral side of peripheral VII in GPIT/RE/09751 and GPIT/RE/09758. These foramina are obscured in all other specimens. Peripherals VIII to XI can have small serrations on the lateral margin, as in GPIT/RE/09731 and GPIT/RE/09735 (Figs. 3 and 7). Peripheral VII contacts costal VI medially. Peripheral IX contacts only costal VII (e.g., GPIT/RE/09739) or costals IV and VII (GPIT/RE/09743). Peripheral X contacts costal VII and VIII medially or only costal VIII (e.g., GPIT/RE/09735 and GPIT/RE/09731). Although GPIT/RE/09747 exhibits a contact between peripheral X and the second suprapygal, this contact is absent in other specimens where this character is discernable. Peripheral XI contacts the pygal and the second suprapygal medially.

Suprapygals and pygal. There are two suprapygals in all specimens. Suprapygal I is small, as wide as long, and similar in size and shape to the last neural bones, by being squarish with parallel or convergent lateral sides. It contacts neural VIII anteriorly, the eighth costal bones laterally, and suprapygal II posteriorly in all specimens for which the contacts can be observed. Suprapygal II is larger than suprapygal I, at least two times wider than long, hexagonal, and crossed posteriorly by the posterior margin of vertebral V and sometimes by the midline sulcus of marginals XII. It contacts suprapygal I anteriorly, the eighth costal bones and eleventh peripherals laterally, and the pygal, posteriorly. Although disarticulated, in GPIT/RE/09731 (Fig. 7) suprapygal II possibly contacts peripheral X laterally. The pygal bone is small, as wide as long, with parallel lateral sides, and has a median notch along the posterior margin, with exception of GPIT/RE/09735, which does not have a notch. As in most crown geoemydids, the pygal is completely intersected by the median sulcus formed by marginals XII. It contacts laterally both peripherals XI and suprapygal II, anteriorly.

Cervical scute. A cervical scute is present in all specimens where the anterior margin of the carapace is intact. The cervical is small, usually as wide as long (longer than wide in GPIT/RE/09738 and GPIT/RE/09744), and has anteriorly convergent lateral sides. In half of specimens (e.g., GPIT/RE/09735, GPIT/RE/09749 and GPIT/RE/09738), a notch is present along the posterior margin of the cervical. Some specimens (e.g., GPIT/RE/09749 and GPIT/RE/09741), by contrast, show a strong anterolateral constriction of the cervical scute (Fig. 6).

Vertebral scutes. There are five vertebral scutes in all specimens, with the exception of GPIT/RE/09738, which presents a small, anomalous scute between vertebrals IV and V (Fig. 9). Vertebral I is quadrate, with convergent or sinuous lateral sides, and has an anterior margin that is always wider than the posterior one. It can be longer than wide, or wider than long. The sulcus between pleural I and vertebral I always contacts the medial portions of marginal I. A small constriction (i.e., an anterolateral step) is present in the anterior region of this sulcus in GPIT/RE/09758 (not figured). Vertebral II is hexagonal, longer than wide, and has lateral sides with equal lengths. The anterior margin crosses neural I and the posterior margin neural III in all specimens. Vertebral III is hexagonal and longer than wide, with exception of GPIT/RE/09743 where it is wider than long. The lateral sides of vertebral III have equal lengths and are almost parallel to each other. The sulcus between vertebral III and pleural II is usually straight (87% of specimens), but sometimes convex (13%). Only GPIT/RE/09747 shows an asymmetry with the left sulcus being straight and the right sulcus being concave. Vertebral IV is hexagonal, usually wider than long, but almost twice as wide than long in GPIT/RE/09743 and longer than wide in

GPIT/RE/09744 and GPIT/RE/09749. The lateral sides are generally of the same length, with exception of GPIT/RE/09738 and GPIT/RE/09743 where the posterior sides are shorter. The anterior margin of vertebral IV always crosses neural V, while the posterior margin generally crosses neural VIII, with exception of GPIT/RE/09738 and GPIT/RE/09747, where it overlaps the suture between neurals VII–VIII. Vertebral V is trapezoidal, more than two times wider than long and with convergent lateral margins that run across costal VIII. GPIT/RE/09747 has an anterior constriction in vertebral V that is unique to that specimen. A large contact between vertebral V and marginals XI is present in GPIT/RE/09743 and GPIT/RE/09747 (Figs. 4 and 11).

Pleural scutes. There are four pairs of pleural scutes in all specimens. Many specimens, adults and juveniles, show growth annuli on the lateral side of the pleurals (e.g., GPIT/RE/09744, GPIT/RE/09735, GPIT/RE/09741, GPIT/RE/09743). Pleural I is the longest pleural and overlaps part of the nuchal, peripherals I–IV, and sometimes peripheral V (GPIT/RE/09738), contacting directly marginal scutes I-IV as well as part of marginal V. The sulcus between pleural I and II is straight or sinuous, but without an anteromedial process, runs across costal II, and always contacts marginal V. Pleural II is rectangular, almost two times wider than long, and overlaps peripherals V–VII, directly contacting marginal VI and part of marginal scutes V and VII. The sulcus between pleural II and III is straight, without an anteromedial process, runs across costal IV, and, as documented by GPIT/RE/09743, contacts marginal VII. Pleural III is quadrate, wider than long, overlaps peripherals VII–VIII and, at least in GPIT/RE/09743, sometimes part of peripheral IX. It contacts partially marginal scutes VII and IX, and completely contacts marginal scute VIII. The sulcus between pleural III and IV runs across costal VI and contacts marginal IX, at least in GPIT/RE/09743. Pleural IV is the smallest and shortest of the pleural scutes, quadrate, and overlaps peripherals IX and X. It partially contacts marginal scutes IX and XI, and completely contacts marginal X. Pleural IV never contacts marginal XII. The sulcus between pleural IV and vertebral V contacts marginal XI, at least as once again documented by GPIT/RE/09743.

Marginal scutes. There are 12 pairs of marginal scutes in all specimens. The contacts with the pleurals are listed above. Marginals I–III are wider than long, do not form serrations, and placed anteriorly on the carapace. Marginal IV is longer than wide, placed anterolaterally on the carapace, and does not lap onto any costal bones. Marginals V–VIII are situated on the sides of the carapace, longer than wide, and do not lap onto any costal bone. Marginals IX–XII are located at the back of the carapace and are wider than long or as wide as long, at least in GPIT/RE/09747 and GPIT/RE/09735.

Plastron. The plastron of *Banhxeochelys trani* has the typical testudinoid configuration composed of an entoplastron, and pairs of epi-, hyo-, hypo- and xiphiplastra. The anterior and posterior plastral lobes are about the same length and width. A well-developed bridge ranges from peripheral IV to VI connecting carapace and plastron. The anterior plastron margin is usually straight (14 out of 18 specimens), but sometimes concave (3 out of 18), or anteriorly convex (GPIT/RE/09742 only). Most specimens lack a medial notch in the anterior plastral margin. At the contact of the gular with the humeral, a pair of anterior ‘spikes’ (i.e., anteriorly directly processes) is present in 78% of specimens, and a lateral inflection is present in 50% of specimens. The posterior plastron margin has a well-developed anal notch, which is usually triangular, with exception of GPIT/RE/09738 (Fig. 9), which has a rounded anal notch. Even the smallest specimens lack fontanelles.

Epiplastra. The epiplastra exhibit a thickened margin in visceral view that extends from the anterior margin until the mid-length of the epiplastra, followed by a posterior step, but not an overhang. No muscular insertion marks and posterolateral processes can be observed on the visceral view of the epiplastra (Fig. 8B).

Entoplastron. The entoplastron is centrally located between the epi- and hyoplastra, rhomboidal, and as long as wide. The anterior and posterior portions, as defined by the epi-hyoplastral suture, are about the same size in 73% of specimens. In other specimens it is either the anterior part larger (10%) or the posterior part is larger (10%). The entoplastron is always intersected by the gularohumeral sulcus anteriorly and by the humeropectoral sulcus posteriorly, either close to its posterior margin (in 8 out of 12 specimens) or just at the posterior margin (in the remaining 4 specimens). The posterior process on the epi-hyoplastron suture is only visible in visceral view in GPIT/RE/09736.

Hyoplastra and hypoplastra. The hyo- and hypoplastra are about the same length and width and longer than wide. The hyoplastra contacts the epiplastra and entoplastron anteriorly, suturally contact peripherals IV and V laterally, and the hypoplastra posteriorly. They are crossed anteriorly by the humeropectoral sulcus and posteriorly by the pectoroabdominal sulcus. The hypoplastra are crossed posteriorly by the abdominofemoral sulcus, suturally contact peripherals V and VI laterally, and the xiphiplastra posteriorly. The inguinal buttress insertion is in the center of the hypoplastra, as seen in GPIT/RE/09736. No lateral keels were observed in any specimen on the hyo- and hypoplastra.

Xiphiplastra. Xiphiplastra are large, longer than wide, and crossed anteriorly by the femoroanal sulcus. A step along the margins of the xiphiplastra is associated with the femoroanal sulcus. The visceral xiphiplastral lip is observed in GPIT/RE/09736, the only specimen where it is possible to see this character. The xiphiplastral lip is short in thickness and wide, like the one in *Rhinoclemmys*.

Plastral scutes. There are each one pair of gular, humeral, pectoral, abdominal, femoral, and anal scutes. No inframarginal scutes (i.e., axillary and inguinal scutes) can be discerned. The gulars are longer than wide. The gulars are less than half as long as the median length of the plastral forelobe. The humerals have the shortest median contact of all scutes, are wider than long, and overlap the epiplastra, entoplastron, and part of hyoplastra. The pectorals are wider than long, almost as long as the gulars along their median contact, and placed entirely on the hyoplastra with exception of a minor overlap onto the posterior portions of the entoplastron in some specimens. The pectoroabdominal sulcus is usually straight along its full length, except in GPIT/RE/09754, which presents a long anterolateral notch. The abdominals have the greatest median contact of all scutes, are almost as wide as long, and overlap part of the hyoplastra posteriorly and more than half of the hypoplastra anteriorly. In GPIT/RE/09743, the left abdominal seems to overlap part of peripherals VI and VII as well. The femorals are wider than long and cover part of hypoplastra posteriorly and less than half of the xiphiplastra anteriorly. The femoroanal sulcus converges anteriorly and contacts the lateral margin of xiphiplastra along a small notch. The anals are large, generally longer than wide (with exception with GPIT/RE/09743, where they are as long as wide, Fig. 11), entirely placed on the xiphiplastra, and not fused with each other along the midline.

PHYLOGENETIC ANALYSIS

Matrix

Our morphological matrix is based on the recently assembled character taxon matrix of Garbin, Ascarrunz & Joyce (2018), which focuses on extant geoemydids and embraces polymorphic character observations. The matrix was modified through the addition of 16 new morphological characters (see Appendix S1 for descriptions) and 12 putative extinct geoemydid species from the Eocene and Oligocene of the northern hemisphere: *Banhxeochelys trani* sp. nov., *Bridgeremys pusilla* (Hay 1908)*, Echmatemys septaria* (Cope 1873), *Echmatemys wyomingensis* (Leidy 1869), *Guangdongemys pingi* Claude et al. 2012, *Hardella siamensis* Claude, Suteethorn & Tong 2007, *Isometremys lacuna* Chow & Yeh 1962, *Mauremys thanhinensis* Claude, Suteethorn & Tong 2007, *Palaeochelys elongata* (Gilmore 1931), *Sharemys hemisphaerica* Gilmore 1931, *Sinohadrianus ezoensis* Shikawa 1953, and *Sinohadrianus sichuanensis* Ping 1929. All fossils were scored based on descriptions and photographs available in the literature (e.g., Claude, Suteethorn & Tong, 2007; Claude et al., 2012), with exception of *Banhxeochelys trani*, and the North American geoemydids *Br. pusilla, E. septaria* and *E. wyomingensis*, which were scored based on first hand observations of relevant material. The "polymorphic" method was preferred (i.e., 0&1; Campbell & Frost, 1993) for coding morphological polymorphic characters. For the complete list of morphological characters, specimens analyzed, and our character taxon matrix, refer to Appendixes S1, S2 and S3, respectively.

Our molecular matrix is also based on the one of Garbin, Ascarrunz & Joyce (2018), with three mitochondrial (12S, cytochrome c oxidase I, cytochrome b) and four nuclear loci (R35 intron, c-mos, Rag1 and Rag2) from the works of Honda et al. (2002), Spinks et al. (2004), and Le & McCord, (2008). For details on sequence alignment and on how this matrix was produced, please refer to Garbin, Ascarrunz & Joyce (2018).

Analysis

We performed a total-evidence analysis (TEA) in TNT (Goloboff & Catalano, 2016) based on the morphological and molecular data. After we merged both matrices in TNT, we performed the analysis with 5000 replicates of random addition sequences, holding up to 1 million trees, followed by a round of TBR branch-swapping from the trees held, and a Nelsen strict consensus. All characters were left with equal weight and morphological characters 3, 11–19, 22, 26, 30, 37, 38, 48, 49, 51, 52, 54–56, 58, 70, 79, 80, 88, 92 and 94 were run ordered (for details, see Appendix S2), following Garbin, Ascarrunz & Joyce (2018). The TEA yielded a total of 3820 most parsimonious trees (MPTs) with 511 hits out of 5000 (some replications overflowed) and a best score of 6717. After the round of TBR, the same best score remained and the number of MPTs held went up to 760375 trees. The strict consensus of all these MPTs is shown in Figure 13.

We then ran the IterPCR script (Pol & Escapa, 2009) to identify rogue species that could be pruned out of the trees in order to gain resolution, followed by a strict consensus. The IterPCR script suggested that all included fossil species should be pruned to gain resolution of 16 nodes, with exception of *G. pingi* and *Ba. trani*. The strict consensus with pruned species is shown in Figure 14.

To investigate the phylogenetic position of each fossil species, we ran the strict consensus again, but this time, we included only one fossil at a time (excluding the other fossils from the consensus calculation, not from the matrix). The summary of the phylogenetic position of the fossils in each consensus is given in Figure 15. *Sharemys hemisphaerica* and the species of *Sinohadrianus* are not shown in this tree as the consensus resulting from their individual analysis was not in agreement with that of other extinct geoemydids (Appendix S4).

For a final run, we ran the Total-Evidence analysis on TNT with the same parameters described above (first paragraph, this session) excluding all fossil taxa with exception of *Ba. trani*. This analysis yielded 8 MPTs with a best score of 6667 and 1743 hits out of 5000 replications. The results were the same after the round of TBR branch-swapping. The Nelsen strict consensus of these 8 MPTs is shown in Figure 16. In this analysis *Ba. trani* had a different position by being placed as sister-taxon to all extant Geoemydidae.

DISCUSSION

Alpha Taxonomy

As geoemydids appeared across the northern hemisphere in the early Eocene (Lapparent de Broin, 2001; Vlachos, 2018; Claude et al., 2012) in near synchrony, it is necessary to compare *Banhxeochelys trani* gen. et sp. nov. to putative Eocene/Oligocene geoemydids across the globe to establish its validity as a new species.

Geoemydids probably dispersed from Asia to North America during the Paleocene–Eocene Thermal Maximum (Lourenço et al., 2012), but their fossil record is mostly restricted to the Eocene. Although nearly two-dozen species were named near the turn of the 19th to 20th century (Hay, 1908), only nine *Echmatemys* species and *Bridgeremys pusilla* are currently recognized as valid (Vlachos, 2018). All known species of *Echmatemys* are characterized by the presence of extremely well developed axillary and inguinal buttresses and hexagonal neurals (Vlachos, 2018) and can therefore be readily distinguished from *Ba. trani*. *Echmatemys haydeni* Leidy 1870b is notable for having octagonal neural IV, but can nevertheless be further differentiated from *Ba. trani* by the absence of keels and more elongate vertebrals, in addition to the presumed presence of well developed axillary and inguinal buttresses.

Banhxeochelys trani differs from the North American *Bridgeremys pusilla* by having a larger adult size (*Br. pusilla* having a maximum plastron length of 13.5 cm; pers. obs.); hexagonal anterolaterally short-sided neurals (only on the seventh and eighth neurals, most neurals are posterolateral in *Br. pusilla*); an octagonal fourth neural (*Br. pusilla* having an octagonal second or third neural); and a well developed anal notch (poorly developed in *Br. pusilla*). In our personal observations of *Br. pusilla* (specimens analyzed in Appendix S1) we further observed a thick xiphiplastral lip and a ventral nuchal lip in this species, both absent in *Ba. trani*. In addition, Vlachos (2018) documents the possible presence of a hinge in *Br. pusilla*, which is also absent in *Ba. trani.*

Geoemydids appear in the early Eocene of Europe as well (Lapparent de Broin, 2001), but it is unclear if they dispersed from Asia or from North America (Joyce et al., 2016). About two dozen species have been named based on material from the Eocene of England, France, and Germany (Lapparent de Broin, 2001), but an alpha taxonomic revision of the group is still outstanding. We here agree with Hervet (2004a, b) and Claude and Tong (2004) that two lineages are present in the Eocene, although we side with Claude and Tong (2004) by seeing less taxonomic diversity. The first lineage ("*Palaeochelys* sensu lato – *Mauremys*" of Hervet, 2004a; *Palaeochelys* of Claude and Tong, 2004) is best represented by rich material from Messel (*Palaeoemys messeliana* [Staesche, 1928]) and Geiseltal (*Borkenia germanica* [Hummel, 1935]), both in Germany, but their taxonomic status and variation are in need of revision. The second lineage ("Ptychogasteridae group" of Hervet, 2004b) is best represented by *Geiselemys ptychogastroides* (Hummel, 1935), also from Geiseltal, Germany. We mostly compare *Banhxeochelys trani* to these species, as they appear to be representative.

Palaeoemys messeliana (*Francellia messeliana* of Hervet, 2004a) differs from *Banhxeochelys trani* by having a small sized carapace (maximum 20 cm), a slight nuchal emargination, weak lateral keels, a lyre-shaped first vertebral with strong anterolateral constriction, hexagonal neurals with anterior short sides, a pygal bone intersected by the posterior margin of the fifth vertebral, and an entoplastron not intersected by the humeropectoral sulcus (Hervet, 2004a; Claude & Tong, 2004). *Borkenia germanica* differs from *Banhxeochelys trani* by having a weak nuchal notch (absent in *Ba. trani*), a hexagonal sixth neural with posterolateral short sides, absence of lateral keels, an entoplastron not overlapped by gular or pectoral scutes, a completely straight anterior plastron margin without any notch, and gular scutes wider than long (Hervet, 2004a). The differences seen in these two species appear to hold true for all other representatives of the *Palaeoemys* lineage.

Banhxeochelys trani differs from *Geiselemys ptychogastroides* by having less thick epiplastral lips, by lacking a posterior step, and shorter lateral spikes on the anterior plastral margin ("ptychogasterid spikes"; strong in *ptychogastroides*). Unlike *Ba. trani, G. ptychogastroides* has an octagonal neural II, and neurals III–VI that are hexagonal with posterior short sides, or sometimes rectangular. These two species have in common an entoplastron intersected posteriorly by the humeropectoral sulcus, a deep anal notch and a moderate xiphiplastral lip, short in thickness (seaming less thick in *Banhxeochelys*).

In Southeast Asia, two geoemydid species have been described from the Early Oligocene Krabi basin in Thailand, *Hardella siamensis and Mauremys thanhinensis* (Claude, Suteethorn & Tong, 2007), proposed to be closely related to extant *Hardella* and *Mauremys* species. Two other geoemydid species, *Guangdongemys pingi* and *Isometremys lacuna* are known from the Late Eocene Maoming basin of China (Claude et al., 2012), a locality 400 km away from the Na

Duong coal mine. *Isometremys lacuna* has been hypothesized to be more closely related to the old-world geoemydids (i.e., “three keeled Geoemydidae” of Claude et al., 2012), than to *Echmatemys* and *Rhinoclemmys*, while *G. pingi* has been hypothesized to have a more basal position within the geoemydid crown clade (Claude et al., 2012).

Banhxeochelys trani differs from *Mauremys thanhinensis* by having a longer median keel that crosses neural I to suprapygal I, shorter lateral keels (crossing costals I to VII or restricted to costals III and IV), neurals with anterior short-sides (posterior in *M. thanhinensis*), a first vertebral scute contacting only the first marginal, wide bridge peripherals, a median notch at the anterior plastral margin, and a thin xiphiplastral lip.

Unlike *Hardella siamensis*, *Banhxeochelys trani* has a longer median keel crossing neural I to suprapygal I, two lateral keels, an octagonal fourth neural, bridge marginal scutes that extend over the hyoplastron, an entoplastron intersected by the humeropectoral sulcus, and a deep triangular anal notch.

Banhxeochelys trani shows several similarities with *Isometremys lacuna*, like the presence of three carapacial keels, neurals II to V about the same size, wide vertebral scutes, a wider than long first vertebral scute, and an entoplastron intersected posteriorly by the humeropectoral sulcus. But unlike *Ba. trani*, *I. lacuna* has all neural bones with anterior short-sides and its median keel is located posteriorly only, crossing neural IV to suprapygal II (in *Ba. trani* it crosses all neurals).

As *Guangdongemys pingi, Ba. trani* has an octagonal fourth neural, the other neurals have anterior short-sides, the first neural is oval or rectangular, and the short costals II–V are about the same length. On the other hand, *G. pingi* does not have carapacial keels, the entoplastron is not intersected by the humeropectoral sulcus, and vertebral I is narrower.

Many geoemydid species have been described from the Eocene/Oligocene of China, Kazakhstan, and Japan (e.g., Gilmore, 1931; Urata, 1968; Chkhikvadze, 1973; Claude & Tong, 2004), but as with the European geoemydid fauna, these species are in need of taxonomic revision (Danilov, 2018).

Of the 11 geoemydid species described from the Eocene–Oligocene of Kazakhstan (Chkhikvadze 1970, 1971, 1973, 1990), we have chosen to compare *Banhxeochelys trani* with "*Echmatemys" orlovi* Chkhikvadze, 1970 and *Zaisanemys borisovi* Chkhikvadze, 1973 (not [sic!] "*Echmatemys" borisovi* Chkhikvadze, 1990) because the remaining species from Kazakhstan are described from small fragments (Danilov, 2018) and therefore do not provide a significant amount of information for comparison (Chkhikvadze 1970, 1971, 1973, 1990).

Zaisanemys borisovi differs from *Banhxeochelys trani* by having narrower epiplastral lips that do not touching medially, a heart-shaped anterior plastral margin with a median notch, and an entoplastron not intersected by the humeropectoral sulcus. "*Echmatemys*" *orlovi* differs from *Banhxeochelys trani* by having a straight anterior plastral margin with strong lateral spikes ("ptychogasterid spikes"), a moderate to thick epiplastral lips (9 mm thick; Chkhikvadze, 1973) that do no meet at epiplastral midline, a moderate xiphiplastral lip, and the presence of axillary and inguinal scutes. As *Ba. trani* and the North American *Echmatemys, E. orlovi* has a deep anal notch (Chkhikvadze, 1973).

Three species are named from the Eocene/Oligocene of China: *Palaeochelys elongata*, *Sharemys hemisphaerica*, and *Sinohadrianus sichuanensis*. *Palaeochelys elongata* differs from *Ba. trani* by the following combination of characters: carapace with a median interrupted keel; variable shape of neurals, such as an octagonal third neural, first neural rectangular, second neural hexagonal with anterolateral short sides, and all other neurals with posterolateral short sides; small size, reaching a maximum carapace length of 24 cm; a great inflection on the margin of the gulohumeral sulcus; entoplastron not intersected by the humeropectoral sulcus; and a large axillary scute (Gilmore, 1931). *Banhxeochelys trani* also shares some similarities with this species, such as the presence of a deep anal notch and gular scutes that are longer than wide (Gilmore, 1931; Brinkman, 2008).

The other Early Oligocene species from China, *Sharemys hemisphaerica*, differs from *Ba. trani* by the following combination of characters: very large subhemisphaerical carapace, no carapacial keels, a well developed nuchal notch, only one suprapygal bone, pygal bone overlapped by the fifth vertebral, wider plastron (bridge to bridge width), anterior plastron margin with a median notch, a strong inflection lateral to the gular scutes, humeropectoral sulcus intersecting the entoplastron, anteriorly to the epi-hyoplastron suture, pectoroabdominal sulcus intersecting part of the hyo-hypoplastron suture, and a very short anal scute (Gilmore, 1931; Brinkman, 2008). Of all the species compared here, this is probably the most distinct species from *Ba. trani*.

Sinohadrianus sichuanensis from the Middle Eocene has a similar neural series shape to that of *Ba. trani*, as both have all hexagonal anterior short-sided neurals, and an octagonal fourth and square fifth neural bone (Ping, 1929; Brinkman, 2008). However, *Ba. trani* is distinguished by having three carapacial keels (absent in *Si. sichuanensis*), costal bones II–VIII with equal length on the inner and outer corners (costals V–VIII have slightly alternating lengths in *Si. sichuanensis*), a short posterior plastral lobe, an entoplastron intersected by the humeropectoral sulcus, and a deeper anal notch.

The Japanese species *Sinohadrianus ezoensis* from the Late Eocene of Hokkaido is known only from the inner cast of the carapace and the exterior part, where only the sulci outline is preserved. This species is distinguished from *Ba. trani* by having all neurals hexagonal with anterior short sides, narrower neural bones, shorter first costal bone, and the presence of two pygal bones, the first half-moon shaped and the second, square.

Of all above mentioned species, *Banhxeochelys trani* is most similar to the Maoming species *G. pingi* and *I. lacuna*. The Na Duong species shares with *G. pingi* the presence of an octagonal fourth neural and remaining neurals hexagonal with anterior short sides, and with *I. lacuna* the presence of three carapacial keels and an entoplastron not intersected by humeropectoral sulcus. It therefore is "intermediate" between these two Maoming species. However, *Ba. trani* does not have particular characteristics that makes it more similar to any Maoming species in particular, and is not phylogenetically closely related to neither *G. pingi* or *I. lacuna* (Figs. 14 and 15). Due to the unique set of characters that are present in this Na Duong material we herein conclude *Banhxeochelys trani* to be a new species.

Intraspecific variation

Intraspecific variation of morphological characters is either associated with gender (i.e., sexual dimorphism), space (i.e., geographic variation), maturity (i.e., ontogenetic variation), pathology (e.g., developmental malformations), phenotypic plasticity (e.g., the development of different morphotypes despite the same genetic basis), or regular genetic variation unrelated to any of the previously listed factors (Ridley, 2006). As paleontologists rely solely on osteological characters, a good understanding of intraspecific variation in skeletal morphology is important to this community, as variation based on genetic differences should be preferred when establishing new species or assessing phylogenetic relationships. Countless studies exist that summarize variation within extant turtle species (e.g., Sánchez-Villagra et al., 1995; Lovich et al., 1998;

Garbin et al., 2016), but these typically focus on externally visible soft-tissue characters and therefore only have limited utility to paleontologists. Notably exception include Minx (1992) and Delfino, Fritz & Sánchez-Villagra (2010), which summarize variation in phalangeal formula in North American box turtles and trionychians, respectively, or Bever (2009a, b), which detail variation and growth in the skull of *Pseudemys texana* and *Sternotherus odoratus*, respectively.

One reason why it is difficult to document skeletal variation in extant turtles is because well-prepared skeletal material is rare in museum collections (Garbin, Ascarrunz & Joyce, 2018). This is generally true for fossils as well, but particularly fossil rich localities or formations often yield large samples of turtles that can be used to document skeletal variation in extinct species. Large numbers of fossil geoemydids (i.e., more than 10 individuals) have previously been reported from the Eocene of Messel, Germany (Cadena, Joyce & Smith, 2018), the Eocene of Geiseltal, Germany (Hummel, 1935), and the Eocene of Wyoming (Gilmore, 1945; Brand et al., 2000), but no study has of yet properly summarized and discussed intraspecific variation based on this material.

We here are able to documented intraspecific variation of *Banhxeochelys trani* based on 30 near complete to complete shell specimens, representing 14 adults (i.e., midline length of hyoplastron greater than 70mm), 8 subadults (i.e., midline length of hyoplastron between 40–70mm), and 8 juveniles (i.e., midline length of hyoplastron less than 40mm; Table 1). As all individuals were collected from a single stratigraphic horizon and appear to represent a single species, we here regard this collection to reflect natural variation found in a natural population.

Out of the 96 characters scored for this species in the phylogenetic analysis, around 40% show some degree of polymorphism. This variation is described in detail above (see Description above) and we just summarize some important characters here.

The most apparent variation we observe in *Ba. trani* pertains to the presence of lateral carapacial keels. In many extant geoemydid (e.g., *Mauremys reevesii*, *Cyclemys dentata, Heosemys spinosa*), juveniles have a three-keeled carapace, but the lateral keels are reduced or even lost completely in subadults and adults (Claude & Tong, 2004; Claude et al., 2012). This appears to be the case as well for *Ba. trani*, as juveniles are tricarinate, while adults lack lateral keels.

We here also attribute changes in the presence of a notch in the anterior plastral margin to ontogenetic variation. In this study, a notch is present in 46% of juveniles and subadults, but only in 22% of adults. This indicates that a notch is commonly present in juveniles but probably gradually disappears during growth, perhaps due to the addition of bony material at the margin of the plastron. This appears to be the first time that ontogenetic variability is documented for this character.

The variation observed in the shape of the neural I (i.e., oval, rectangular, or triangular) is in agreement with that observed in other geoemydid species (Garbin, Ascarrunz & Joyce, 2018), as well as that observed in other cryptodires (Pritchard, 1988). Two specimens (i.e., GPIT/RE/09759 and GPIT/RE/09748) have a continuous series of hexagonal neurals with anterior short sides, which differs from the common condition of *Ba. trani*, where the series is pierced by an octagonal fourth neural and a square or rounded fifth neural.

Most specimens of *Ba. trani* have an entoplastron that is as long as wide, with anterior and posterior halves of about the same size. However, in three specimens (GPIT/RE/09754, GPIT/RE/09736 and GPIT/RE/09738) the anterior part of the entoplastron is larger, and in two other specimens (GPIT/RE/09752 and GPIT/RE/09755) the posterior part is larger. We conclude that these are abnormalities or random variations, as there does not seem to be a correlation between this variation and the specimens. Although always intersected posteriorly by the humeropectoral sulcus, another variation observed in the entoplastron is the exact place of this intersection. In 67% of specimens, the sulcus crosses the most posterior suture of the entoplastron (in some way overlapping the ento-hyoplastron suture), and in 33% of specimens the intersection is between the epi-hyoplastron suture and the posterior suture of the entoplastron.

Most geoemydids, and testudinoids in general, can show sexual dimorphic characters in shell morphology (Ernst & Barbour, 1989). While males of terrestrial and semi-aquatic species usually have concave plastra, females tend to have flat ones (Pritchard, 1979). Carapace maximum length also varies between sexes, with females being up to three times longer than males in some species (e.g., *Hardella thurjii*; Pritchard, 1979). For other groups of turtles (like stem and crown pleurodires) other sexual dimorphic characteristics may apply, such as the presence of a more domed carapace and a narrower but broader anal notch in females (Ernst & Barbour, 1989; Sullivan & Joyce, 2017). The specimens in our sample of *Ba. trani* are either not sufficiently complete and/or show massive deformation, and we are therefore not able to determine the sex of specimens or distinguish between sexual related characteristics in adults. We finally also cannot comment on geographic variation of *Ba. trani*, as all specimens are from a single quarry.

Phylogenetic relationships

When the total-evidence matrix of 96 morphological characters and 7 molecular loci is run with all fossil taxa deactivated, the fully resolved reference tree of Garbin, Ascarrunz & Joyce (2018, not shown) is retrieved, in which Geoemydidae is found as monophyletic relative to Testudinidae. When all fossils are activated, the strict consensus neither shows a clear phylogenetic position for *Banhxeochelys trani* nor any of the other putative extinct geoemydid species included (Fig. 13). This poorly resolved consensus furthermore only retrieves some extant clades as monophyletic, such as *Cuora*, *Rhinoclemmys*, and *Heosemys*, but not others, such as *Pangshura* and *Batagur*. After pruning all extinct species but *Banhxeochelys trani* and *Guangdongemys pingi* from the consensus, the resolution improves by 16 nodes (Figure 14). In this consensus, all main extant geoemydid clades are retrieved as monophyletic (e.g., *Pangshura*, *Batagur*, *Mauremys*, *Cuora*) and *G. pingi* has a clear position as sister to *Geoclemys hamiltonii*, supported by a first vertebral scute that is longer than wide. *Banhxeochelys trani*, however, is still found in a polytomy at the base of Testuguria together with *Malayemys, Orlitia*, *Siebenrockiella*, and Testudinidae. The polytomy among extant testugurians is retained even when all fossils are pruned from the consensus (not shown). It is therefore clear that the inclusion of fossils negatively impacted resolution among extant taxa.

We here for the first time investigate the phylogenetic position of some putative Paleogene geoemydids in an explicit phylogenetic context. Until now, species had either never been phylogenetic investigated, or had been manually placed in molecular trees using hypothesized synapomorphies (i.e., Claude & Tong, 2004; Claude et al., 2012). As all fossils are placed in a basal polytomy in the total evidence analysis, we here investigate their phylogenetic placement individually by pruning all fossils but one from a series of consensus trees compiled from the total evidence analysis (summarized in Figure 15). We discuss below the phylogenetic position of each fossil species in these consensus trees and highlight morphological characters that support~~ing~~ these placements. We do not assert this scenario to be the most correct hypothesis for geoemydid evolution, but as an additional step towards the comprehension of the evolutionary history of Testudinoidea.

In all consensuses, the ingroup clade (Testuguria) is supported by the following characters: presence of anterior and posterior musk duct foramina, pygal bone completely divided by the twelfth marginal sulcus, gular scute as long as wide (or wider than long), anterior region of the entoplastron larger than the posterior, and a deep anal notch. Again, these synapomorphies are not exclusive to all species. For example, both testudinid species *Stigmochelys pardalis* and *Gopherus polyphemus*, have a pygal bone that is not divided by the twelfth marginal sulcus, and some geoemydid species (e.g., *Leucocephalon yuwonoi* McCord, Iverson & Boeadi, 1995; *Rhinoclemmys areolata* Duméril & Bibron, 1851) have ~~it~~ incompletely divided one.

The branch of *Banhxeochelys trani* is autapomorphically supported by the presence of lateral keels that are extending from the first to fourth pleural scute, an epiplastral lip that extends until the mid-length of the epiplastron or closer to the entoplastron, and no distinct processes at the hypo-xiphiplastral suture and at the epi-hyoplastron suture.

The position of *Guangdongemys pingi* as sister to *Geoclemys hamiltonii* is supported by a first vertebral scute that is longer than wide. The other Maoming species, *Isometremys lacuna*, is placed at the base of Testuguria and its branch is supported by the presence of three carapacial keels, a median keel placed posteriorly (along third, fourth and fifth vertebral scutes), posterior marginals VIII–XII that are not flared, and an entoplastron that is larger posteriorly.

Although the Krabi species *Mauremys thanhinensis* and *Hardella siamensis* present characters that could be attributed to extant genera inside crown clade Geoemydidae (e.g., contact between first vertebral and second marginal for *Mauremys*; and vertebral scutes that are as long as wide for *Hardella*; Claude, Suteethorn & Tong, 2007; Garbin, Ascarrunz & Joyce, 2018), both were recovered at the base of Testuguria, as sisters to Testudinidae, Geoemydinae, Batagurinae, and other fossil geoemydids. *Mauremys thanhinensis* is autapomorphically supported by the presence of three carapacial keels, a posterior median keel, posterior marginals VIII–XII that are not flared, a fourth vertebral scute that is as long as wide, inguinal buttress insertion at fourth costal, humeropectoral sulcus intersecting the ento-hyoplastron suture, and subequal entoplastron areas (as defined by the epi-hyoplastron suture contact). The autapomorphies of *Hardella siamensis* are a posterior median keel, second pleural contacting the sixth marginal, a fourth vertebral scute as long as wide, no axillary and inguinal scutes, and a rectangular anal notch.

The North American species of *Echmatemys* and *Bridgeremys pusilla* were all placed along the base of Testuguria. *Bridgeremys pusilla* is autapomorphically supported by a cervical scute notched at the posterior margin, a ventral nuchal lip, a first vertebral scute that is longer than wide, anterior musk duct foramina on the axillary buttress, posterior musk duct foramina on the eighth peripheral, a long epiplastral lip that almost reaches the epi-entoplastron suture, presence of a step posterior to the epiplastral lip, an entoplastron not intersected by the gularohumeral sulcus, and entoplastron anterior and posterior regions that are subequal. The amount of autapomorphies supporting the branch of *Br. pusilla* reflects the uniqueness of this small Eocene species, that was correctly removed from *Echmatemys* by Hutchison (2006). In a recent analysis, these taxa were retrieved in a more derived position near *Mauremys* (Vlachos 2018), but it is difficult to compare results, as the data matrices used differ substantially in character and taxon sampling. In either case, both taxa are not associated with *Rhinoclemmys*, which implies the independent dispersal of geoemydids from Asia to North America.

Echmatemys wyomingensis is supported by the presence of a posterior median keel, posterior marginals that are not flared, a cervical scute notched posteriorly, anterior plastral margin without spikes, epiplastral lip reaching the mid-length of the epiplastron, and the presence of a step posterior to the epiplastral lip. *Echmatemys septaria*, by contrast, is supported by the absence of carapacial keels, flared posterior marginals, the presence of a ventral nuchal lip, sulcus between first and second pleural contacting sulcus between fourth and fifth marginals, pygal bone without a posterior notch, epiplastral lip reaching closer to the epi-entoplastron suture, the presence of a step posterior to the epiplastral lip, epi-hyoplastron suture without distinct processes, and an entoplastron with anterior and posterior regions about the same size. Interestingly, if the analysis is run including these two taxa as the only active fossils, they are not retrieved as monophyletic.

Palaeochelys elongata, as *Guangdongemys pingi*, is the only Paleogene species recovered as closely related to extant geoemydids (Fig. 15). The position of *P. elongata* inside Geoemydinae is supported by third and fifth neurals with posterior short sides, an inguinal buttress inserted at the fifth costal bone, and absence of inguinal scutes (as opposed to the presence of this scute in Batagurinae). The *P. elongata* branch is supported by an anterior plastral margin without lateral spikes (i.e., ptychogasterid spikes) and subequal anterior and posterior parts of the entoplastron.

Three extant geoemydids, *Malayemys, Orlitia borneensis*, and *Siebenrockiella crassicollis* were recovered along the base of Testuguria in all consensuses, with exception of the strict consensus trees that included *Sinohadrianus sichuanensis* or *Sharemys hemisphaerica* (Appendix S4, Figs. 1 and 2). In these trees, *Malayemys* is placed as sister to *Orlitia borneensis* at the base of Palatochelydia. Their placement there and as sister to each other is supported by molecular signal only. In the *Si. sichuanensis* consensus, *Siebenrockiella crassicollis* is placed as sister to all palatochelydians, which is supported by many molecular characters as well as the presence of a fifth neural with anterior short sides. In the *Sh. hemisphaerica* consensus (Appendix S4, Fig. 2), *Siebenrockiella crassicollis* is recovered along the base with other extant species.

As it is possible that the coding of some of the fossil taxa included in this analysis includes errors resulting from various taphonomic processes (crushing, preparation, imaging), we ran a final analysis that activates *Ba. trani* as the only fossil taxon. In this analysis *Ba. trani* is retrieved as a pan-geoemydid species as sister to all extant geoemydids (Figure 16). This placement is supported in all eight MPTs and in the strict consensus (Fig. 16), by the presence of anterior and posterior musk duct foramina, a character that is usually considered to be a synapomorphy for (crown) Geoemydidae (Hirayama, 1985; Yasukawa *et al.*, 2001; Le & McCord, 2008). As other groups of testudinoids possess musk duct foramina as well, we are with Garbin, Ascarrunz & Joyce (2018) that better sampling of basal taxa is needed to confidently clarify the use of this character in diagnosing geoemydids. This study at least recovers the presence of musk duct foramina as a synapomorphy of Pan-Geoemydidae (*Banhxeochelys* + crown group) and the presence of gular scutes that are wider than long instead as a non-exclusive synapomorphy of crown Geoemydidae.

The large polytomy at the base of Testuguria does not imply that the phylogenetic position of the putative fossil geoemydids included in the analysis is not known at all. Instead, it is important to note that all strict consensus trees include large clades of extant geoemydids that affirmatively do not include these fossils. We therefore can have high confidence that most of these Paleogene taxa indeed represent basal testugurians or geoemydids, not derived representatives of Palatochelydia or Geoemydinae. This, in return, is consistent with an early Paleogene divergence scenario as predicted by several molecular calibration analyses (e.g., Lourenço et al., 2012; Joyce et al. 2013; Pereira et al. 2017).

Palaeoecology

A sample of more than 100 shells of *Banhxeochelys trani* was collected from lacustrine lignitic shales (layer 80) in Na Duong formation (Böhme et al., 2013). The large lake ~~have~~ been anoxic at bottom waters and was inhabited by diverse fish and crocodile species (Böhme et al., 2011, 2013).

There are no signs that the specimens of *Ba. trani* studied herein were transported to the site where they were deposited, as the majority of specimens are articulated (in contrast to terrestrial mammals) and show no signs of mechanical erosion. We therefore interpret *Ba. trani* as a largely aquatic turtle. To a certain degree it may be possible to distinguish more terrestrial habitat preferences from more aquatic ones using skull shape (Claude et al., 2004), limb proportions (Joyce & Gauthier, 2004), or shell morphology (Pritchard, 1979), but as no skull or limbs are present and all shells fully crushed, these sources of information cannot be used to further clarify the ecological habits of *Ba. trani*. We cannot speculate about dietary preferences, although it is notable that the Na Duong site has yielded an exceptionally diverse flora and fauna (Böhme et al., 2013) that certainly could support the full spectrum of dietary preferences observed in extant testudinoids.

Despite the great numbers of recovered shells, there is no evidence for gregarious behavior in *Ba. trani*. The fossils were excavated evenly distributed over an area of approximately 10.000 m^2, at a rate of one individual per 100 m^2. Only a single shell accumulation was found (fig. 14 in Böhme et al., 2011), which is composed of fish remains, a crocodile tooth, six geoemydids, and a trionychid shell. Crocodile bite marks on the shells led to the conclusion that this unique accumulation may represent a crocodile regurgitate (Böhme et al., 2013). Geoemydid and trionychid turtles therefore represent an important food source for the Na Duong crocodiles.

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REFERENCES

Batsch AJGC. 1788. *Versuch einer Anleitung, zur Kenntniß und Geschichte der Thiere und Mineralien*. Jena: Akademische Buchhandlung.

Bever G. 2009a. The postnatal skull of the extant North American turtle *Pseudemys texana* (Cryptodira: Emydidae), with comments on the study of discrete intraspecific variation. *Journal of Morphology* **270:**97–128.

Bever G. 2009b. Postnatal ontogeny of the skull in the extant North American turtle *Sternotherus odoratus* (Cryptodira: Kinosternidae). *Bulletin of the American Museum of Natural History* **330:**1–97.

Böhme M, Prieto J, Schneider S, Hung NV, Quang DD, Tran, DN. 2011. The Cenozoic on-shore basins of Northern Vietnam: biostratigraphy, vertebrate and invertebrate faunas. *Journal of Asian Earth Sciences* **40:**672–687.

Böhme M, Aiglstorfer M, Antoine P-O, Appel E, Havlik P, Métais G, Phuc LT, Schneider S, Setzer F, Tappert R, Tran DN, Uhl D, Prieto J. 2013. Na Duong (northern Vietnam) –

an exceptional window into Eocene ecosystems from Southeast Asia. *Zitteliana A* **53:**120–167.

Brand LR, Goodwin HT, Ambrose PD, Buchheim HP. 2000. Taphonomy of turtles in the Middle Eocene Bridger Formation, Southwest Wyoming. *Palaeogeography, Palaeoclimatology, Palaeoecology* **162:**171–189.

Brinkman DB. 2008. Testudines. In: Li J, Wu X, Zhang F, eds. *The Chinese Fossil Reptiles and Their Kin*. Beijing: Science Press, 35–102.

Cadena E, Joyce WG, Smith KT. 2018. Turtles. In: Schaal S, Smith KT, Habersetzer J, eds. *Messel – A Tropical Fossil Ecosystem*. Basel, Schweizerbart.

Campbell JA, Frost DR. 1993. Anguid lizards of the genus *Abronia*: revisionary notes, descriptions of four new species, a phylogenetic analysis, and key. *Bulletin of the American Museum of Natural History* **216:**1–122.

Chkhikvadze VM. 1970. The oldest Cenozoic turtles of the USSR. *Soobshcheniya Akademii Nauk Gruzinskoi SSR* **60:**749–752.

Chkhikvadze VM. 1971. New turtles of the Oligocene of Kazakhstan and the systematic position of some fossil species of Mongolia. *Bulletin of the Academy of Sciences of the Georgian SSR* **62:**489–492.

Chkhikvadze VM. 1973. *Tertiary turtles of the Zaisan depression*. Tbilisi: Metsniereba Publishers.

Chkhikvadze VM. 1990. *Paleogene turtles of USSR.* Tbilisi: Metsniereba Publishers.

Chow MC, Yeh HK. 1962. A new emydids from Eocene of Maoming Kwangtung. *Vertebrata Palasiatica* **6:**225–229.

Claude J, Tong H. 2004. Early Eocene testudinoid turtles from Saint-Papoul, France, with comments on the early evolution of modern Testudinoidea. *Oryctos* **5:**3–45.

Claude J, Pritchard P, Tong H, Paradis E, Auffray J-C. 2004. Ecological correlates and evolutionary divergence in the skull of turtles: a geometric morphometric assessment. *Systematic Biology* **53:**933–948.

Claude J, Suteethorn V, Tong H. 2007. Turtles from the late Eocene – early Oligocene of the Krabi Basin (Thailand). *Bulletin de la Société Géologique de France* **178:**305–316.

Claude J, Zhang J-Y, Li J-J, Mo J-Y, Kuang X-W, Tong H. 2012. Geoemydid turtles from the Late Eocene Maoming basin, southern China. *Bulletin de la Société Géologique de France* **183:**641–651.

Cope ED. 1868. On the origin of genera. *Proceedings of the Academy of Natural Sciences of Philadelphia* **20:**242–300.

Cope ED. 1873. On the extinct vertebrata of the Eocene of Wyoming observed by the expedition of 1872, with notes on the geology. In: Hayden FV, ed. *Sixth Annual Report of the United States Geological Survey of the Territories*. Washington, United States of America: Government Printing Office, 545–649.

Danilov IG. 2005. Die fossilen Schildkröten Europas. In: Fritz U, ed*. Handbuch der Reptilien und Amphibien Europas.* Wiebelsheim, Aula-Verlag, 329–441.

Danilov IG. 2018. Fossil Reptiles and Birds – Part 4. In: Vorobyeva EI, Lopatin AV, Shishkin MA, eds. *Fossil Vertebrates of Russia and Adjacent Countries*. Moscow: GEOS.

Delfino M, Fritz U, Sánchez-Villagra MR. 2010. Evolutionary and developmental aspects of phalangeal formula variation in pig-nose and soft-shelled turtles (Carettochelyidae and Trionychidae). *Organisms, Diversity & Evolution* **10:**69–79.

Duméril AMC, Bibron G. 1851. *Emys areolata, Emys berardii, Cinosternon leucostomum, Cinosternon cruentatum*. In: Duméril AMC, Duméril AHA, eds. *Catalogue méthodique de la collection des reptiles (Muséum d'Histoire Naturelle de Paris)*. Paris: Gide & Baudry.

Ernst CH, Barbour RW. 1989. *Turtles of the World*. Washington DC: Smithsonian Institution Press.

Fitzinger LJ. 1826. Neue Classification der Reptilien, nach ihren natürlichen Verwandtschaften nebst einer Verwandtschafts–Tafel und einem Verzeichnisse der Reptilien–Sammlung des k.k. Zoologischen Museum zu Wien. Wien: J.G. Hübner Verlag.

Garbin RG, Karlguth DT, Fernandes DS, Pinto RR. 2016. Morphological variation in the Brazilian Radiated Swamp turtle *Acanthochelys radiolata* (Mikan, 1820) (Testudines: Chelidae). *Zootaxa* **4105**:45–64.

Garbin RG, Ascarrunz EA, Joyce WG. 2018. Polymorphic characters in the reconstruction of the phylogeny of geoemydid turtles. *Zoological Journal of the Linnean Society* zlx106. DOI: 10.1093/zoolinnean/zlx106

Gilmore CW. 1931. Fossil turtles of Mongolia. *Bulletion of the American Museum of Natural History* **59:**213–257.

Gilmore CW. 1945. A slab of fossil turtles from Eocene of Wyoming, with notes on the genus *Echmatemys*. *American Journal of Sience* **243:**102–107.

Goloboff PA, Catalano SA. 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* **32:**221–238.

Hay OP. 1908. The fossil turtles of North America. *Carnegie Institution of Washington Publication* **75:**1–568.

Hervet S. 2004a. Systematic of the “*Palaeochelys* sensu lato – *Mauremys*” group (Chelonii, Testudinoidea) from the Tertiary of Western Europe: principal results. *Annales de Paléontologie* **90:**13–78.

Hervet S. 2004b. A new genus of Ptychogasteridae (Chelonii, Testudinoidea) from the Geiseltal (Lutetian of Germany). *Comptes Rendus Palevol* **3:**125–132.

Hervet S. 2006. The oldest European ptychogasterid turtle (Testudinoidea) from the lowermost Eocene amber locality of Le Quesnoy (France, Ypresian, MP7). *Journal of Vertebrate Paleontology* **26:**839–848.

Hirayama R. 1985. Cladistic analysis of batagurine turtles. *Studia Palaeocheloniologica* **1:**140–157.

Honda M, Yasukawa Y, Hirayama R, Ota H. 2002. Phylogenetic relationships of the Asian box turtles of the genus *Cuora* sensu lato (Reptilia: Bataguridae) inferred from mitochondrial DNA sequences. *Zoological Sciences* **19:**1305–1312.

Hummel K. 1935. Schildkröten aus der mitteleozänen Braunkohle des Geiseltales. *Nova Acta Leopoldina* **2:**457–483.

Hutchison JH. 2006. *Bridgeremys* (Geoemydidae: Testudines), a new genus from the middle Eocene of North America. *Russian Journal of Herpetology* **13(Suppl.):**63–83.

Joyce WG, Bell CJ. 2004. A review of the comparative morphology of extant testudinoid turtles (Reptilia: Testudines). *Asiatic Herpetological Research* **10:**53–109.

Joyce WG, Parham JF, Gauthier JA. 2004. Developing a protocol for the conversion of rank-based taxon names to phylogenetically defined clade names, as exemplified by turtles. *Journal of Paleontology* **78:**989–1013.

Joyce WG, Parham JF, Lyson TR, Warnock RCM, Donoghue PCJ. 2013. A divergence dating analysis of turtles using fossil calibrations: an example of best practices. *Journal of Paleontology* **87:**612–634.

Joyce WG, Rabi M, Clark JM, Xu X. 2016. A toothed turtle from the Late Jurassic of China and the global biogeographic history of turtles. *BMC Evolutionary Biology* **16:**236–264.

Lapparent de Broin F. 2001. The European turtle fauna. *Dumerilia* **4:**155–217.

Le M, McCord WP. 2008. Phylogenetic relationships and biogeographical history of the genus *Rhinoclemmys* Fitzinger, 1835 and the monophyly of the turtle Geoemydidae (Testudines: Testudinoidea). *Zoological Journal of the Linnean Society* **153:**751–767.

Leidy J. 1869. Notice of some extinct vertebrates from Wyoming and Dakota. *Proceedings of the Academy of Natural Sciences of Philadelphia* **21:**63–67.

Leidy J. 1870b. Attention to some fossils. *Proceedings of the Academy of Natural Sciences of Philadelphia* **22:**3–5.

Lourenço JM, Claude J, Galtier N, Chiari Y. 2012. Dating cryptodiran nodes: origin and diversification of the turtle superfamily Testudinoidea. *Molecular Phylogenetics and Evolution* **62:**496–507.

Lovich JE, Ernst CH, Zappalorti RT, Herman DW. 1998. Geographic variation in growth and sexual size dimorphism of bog turtles (*Clemmys muhlenbergii*). *The American Midland Naturalist* **139:**69–78.

McCord WP, Iverson JB, Boeadi. 1995. A new batagurid turtle from northern Sulawesi, Indonesia. *Chelonian Conservation and Biology* **1:**311–316.

Minx P. 1992. Variation in phalangeal formulae in the turtle genus *Terrapene*. *Journal of Herpetology* **26:**234–238.

Pereira AG, Sterli J, Moreira FRR, Schrago CG. 2017. Multilocus phylogeny and statistical biogeography clarify the evolutionary history of major lineages of turtles. *Molecular Phylogenetics and Evolution* **113:**59–66.

Ping C. 1929. A new fossil land turtle from Honan. *Bulletin of the Geological Society of China* **8:**231–242

Pol D, Escapa IH. 2009. Unstable taxa in cladistic analysis: identification and the assessment of relevant characters. *Cladistics* **25:**515–527.

Pritchard PCH. 1979. *Encyclopedia of Turtles*. Neptune City, New Jersey: T.F.H. Publications.

Pritchard PCH. 1988. A survey of the neural bone variation among recent chelonian species, with functional interpretations. *Acta Zoologica Cracoviensia* **31:**625–686.

Ridley M. 2006. *Evolution*. New Jersey: Blackwell Publishing.

Sánchez-Villagra MR, Pritchard PCH, Paolillo A, Linares OJ. 1995. Geographic variation in the Matamata turtle, *Chelus fimbriatus*, with observations on its shell morphology and morphometry. *Chelonian Conservation and Biology* **1:**293–300.

Shikawa T. 1953. On a new land turtle from Paleogene of Hokkaido. *Transactions and Proceedings of the Palaeontological Society of Japan* **9:**19–26.

Spinks PQ, Shaffer HB, Iverson JB, McCord WP. 2004. Phylogenetic hypotheses for the turtle family Geoemydidae. *Molecular Phylogenetics and Evolution* **32:**164–182.

Staesche K. 1928. Sumpfschildkröten aus hessischen Tertiärablagerungen. *Abhandlungen der hessischen Geologischen Landesanstalt zu Darmstadt* **8:**5–72.

Sukhanov VB. 2000. Mesozoic turtles of Middle and Central Asia. In: Benton MJ, Shishkin MA, Unwin DM, Kurochkin EV, eds. *The Age of Dinosaurs in Russia and Mongolia*. Cambridge, Cambridge University Press, 309–367.

Sullivan PM, Joyce WG. 2017. The shell and pelvic anatomy of the Late Jurassic turtle *Platychelys oberndorferi* based on material from Solothurn, Switzerland. *Swiss Journal of Palaeontology* **136:**323–343.

[TTWG] Turtle Taxonomy Working Group. 2017. Turtles of the world: annotated checklist and atlas of taxonomy, synonymy, distribution and conservations status (8th edition). *Chelonian Research Monographs* **7:**1–292.

Urata H. 1968. Fossil land turtles form the Karatsu coal field, Saga Prefecture, Kyushu, Japan. *Reports on Earth Science, General Education Kyushu University* **15:**19–44.

Vlachos E. 2018. A review of the fossil record of North American turtles of the clade Pan-Testudinoidea. *Bulletin of the Peabody Museum of Natural History* **59:**3–94.

Yasukawa Y, Hirayama R, Hikida T. 2001. Phylogenetic relationships of geoemydine turtles (Reptilia: Bataguridae). *Current Herpetology* **20:**105–133.

Table 1(on next page)

Measurement of shells of *Banhxeochelys trani* from specimens described in this study.

All measurements are reported in mm. Scute and bone nomenclature are in agreement with the text. ML stands for mid length; MxL stands for maximum length. CML is carapace mid length. PML is plastron mid length. Maturity stages are defined in the text; AD (adult), JV (juvenile) and SB (subadult). Abbreviations: *Ab*, abdominal scute; *CoI*, first costal bone; *Hypo*, hypoplastron; *NeIII*, third neural bone; *VeIII,* third vertebral scute.

Specimen	Maturity	CML	VeIII ML	CoI MxL	NeIII MxL	PML	Ab ML	Hypo ML
GPIT/RE/09731	AD	282	52	43	24	237	57	75
GPIT/RE/09732	AD	>305		56	33			85
GPIT/RE/09733	AD		55	49	29		65	78
GPIT/RE/09734	AD			45	31	235		70
GPIT/RE/09735	AD	288	55	53	28	260		78
GPIT/RE/09736	AD					260		73
GPIT/RE/09737	AD			56	33			79
GPIT/RE/09738	AD	292	58	46		272	68	79
GPIT/RE/09739	JV			26	14		34	38
GPIT/RE/09740	JV		27	27				40
GPIT/RE/09741	JV		28	22			40	43
GPIT/RE/09742	JV			21	11			30
GPIT/RE/09743	JV	170	30	30		155	37	42
GPIT/RE/09744	JV		29	28	17			47

GPIT/RE/09745	SB		39	43	23		61
GPIT/RE/09746	SB			41	25		60
GPIT/RE/09747	SB						56
GPIT/RE/09748	SB			38	24		62

Figure 1(on next page)

Map of Southeast Asia showing Paleogene localities that yielded geoemydid turtles.

Stars: Maoming basin, China (Late Eocene); Krabi basin, Thailand (Late Eocene – Early Oligocene); Na Duong basin, Vietnam (Middle to Late Eocene).


100°
110°
120°
25°
20°
15°
10°
CHINA
MYANMAR
Na Duong
Maoming
Hanoi
LAOS
THAILAND
CAMBODIA
VIETNAM
SOUTH CHINA SEA
Gulf of Thailand
Krabi
0
250
500 km

Figure 2(on next page)

GPIT/RE/09760, *Banhxeochelys trani* gen. et sp. nov., holotype, subadult, Middle to Late Eocene (Priabonian) of Vietnam.

(A) Photograph of carapace. (B) Illustration of carapace. (C) Photograph of plastron. (D) Illustration of plastron. Abbreviations: *An*, anal scute; *co*, costal; *epi*, epiplastron; *Gu*, gular scute; *Hu*, humeral scute; *hyo*, hyoplastron; *Ma*, marginal scute; *mdf*, musk duct foramen; ne, neural; *nu*, nuchal; *per*, peripheral; *spy*, suprapygal; *Ve*, vertebral scute; *xi*, xiphiplastron.

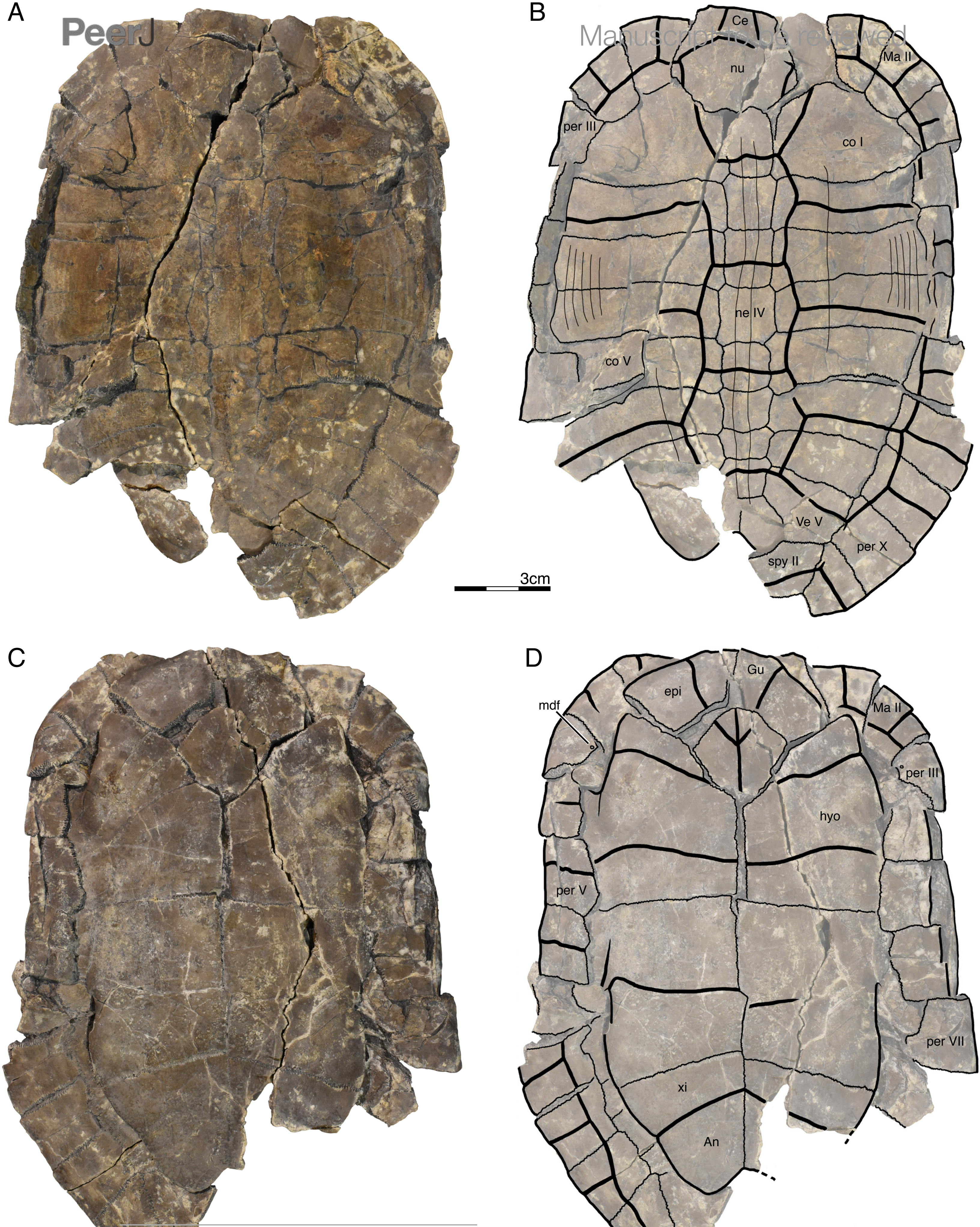
A
B
Ce
nu
Ma II
per III
co I
ne IV
co V
Ve V
per X
spy II
3cm
C
D
Gu
epi
mdf
Ma II
per III
hyo
per V
per VII
xi
An

Figure 3(on next page)

GPIT/RE/09735, *Banhxeochelys trani* gen. et sp. nov., adult, Middle to Late Eocene of Vietnam.

(A) Photograph of carapace. (B) Illustration of carapace. (C) Photograph of plastron. (D) Illustration of plastron. Abbreviations: *An*, anal scute; *co*, costal; *ent*, entoplastron; *epi*, epiplastron; *Gu*, gular scute; *Hu*, humeral scute; *hyo*, hyoplastron; *Ma*, marginal scute; *ne*, neural; *nu*, nuchal; *per*, peripheral; *spy*, suprapygal; *Ve*, vertebral scute.

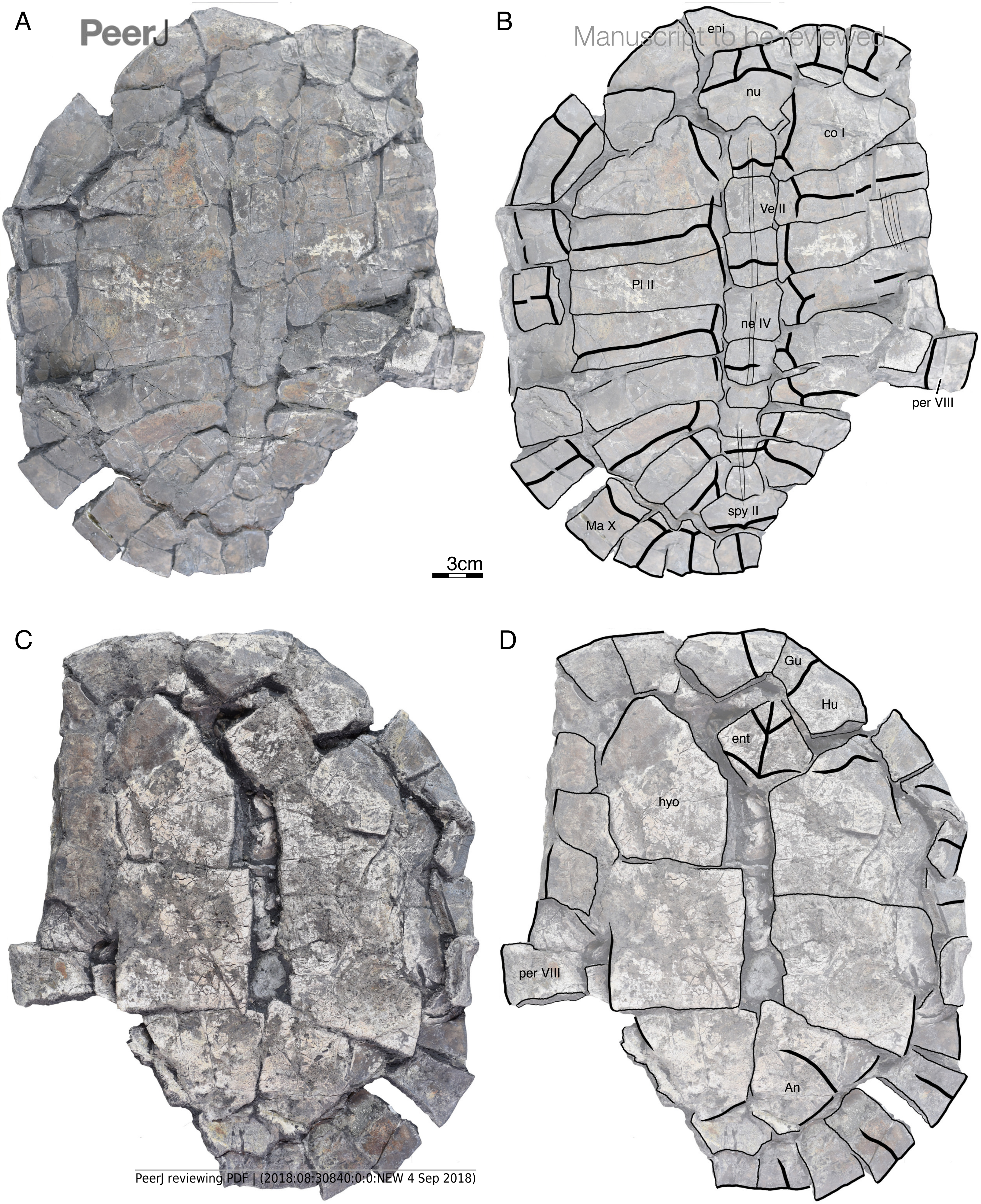
A
B
epi
nu
co I
Ve II
Pl II
ne IV
per VIII
Ma X
spy II
3cm
C
D
Gu
Hu
ent
hyo
per VIII
An

Figure 4(on next page)

GPIT/RE/09747, *Banhxeochelys trani* gen. et sp. nov., subadult, Middle to Late Eocene of Vietnam.

(A) Photograph of carapace. (B) Illustration of carapace. (C) Photograph of plastron. (D) Illustration of plastron. Abbreviations: *Ab*, abdominal scute; *An*, anal scute; *Ma*, marginal scute; *ne*, neural; *per*, peripheral; *Pl*, pleural scute; *py*, pygal; *Ve*, vertebral scute; *xi*, xiphiplastron.

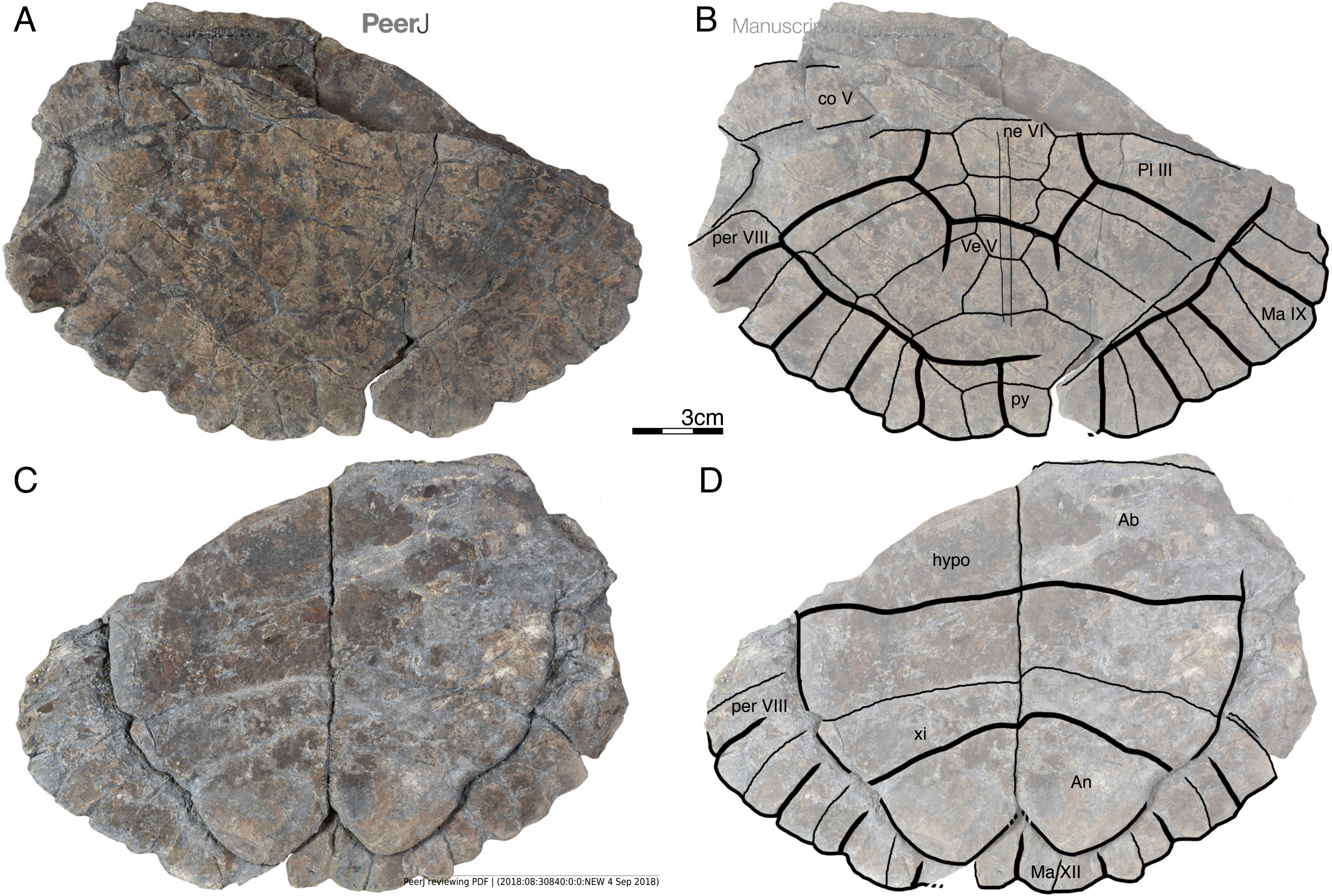
A
B
co V
ne VI
Pl III
per VIII
Ve V
Ma IX
py
3cm
C
D
Ab
hypo
per VIII
xi
An
Ma XII

Figure 5(on next page)

GPIT/RE/09733, *Banhxeochelys trani* gen. et sp. nov., adult, Middle to Late Eocene of Vietnam.

(A) Photograph of carapace. (B) Illustration of carapace. (C) Photograph of plastron. (D) Illustration of plastron. Abbreviations: *Ab*, abdominal scute; *An*, anal scute; *Ce*, cervical scute; *co*, costal; *ent*, entoplastron; *epi*, epiplastron; *Gu*, gular scute; *Hu*, humeral scute; *ne*, neural; *nu*, nuchal; *per*, peripheral; *Pl*, pleural scute; *Ve*, vertebral scute; *xi*, xiphiplastron.

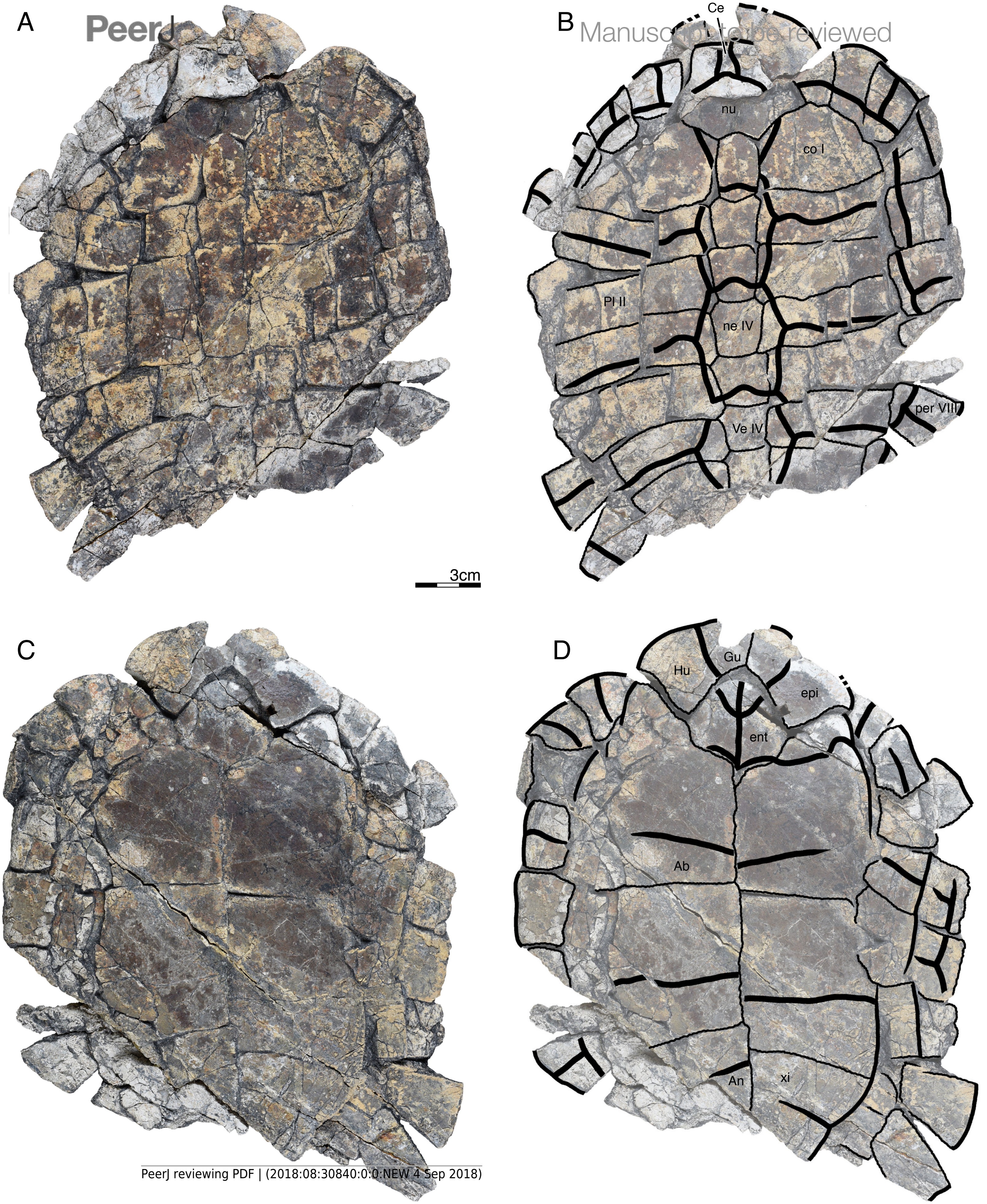
A
B
Ce
nu
co I
Pl II
ne IV
Ve IV
per VIII
3cm
C
D
Hu
Gu
epi
ent
Ab
An
xi

Figure 6(on next page)

GPIT/RE/09749, *Banhxeochelys trani* gen. et sp. nov., subadult, Middle to Late Eocene of Vietnam.

(A) Photograph of carapace. (B) Illustration of carapace. Abbreviations: *Ce*, cervical scute; *co,* costal; *epi*, epiplastron; *Gu*, gular scute; *ne*, neural; *per*, peripheral; *Pl*, pleural scute; *Ve*, vertebral scute.

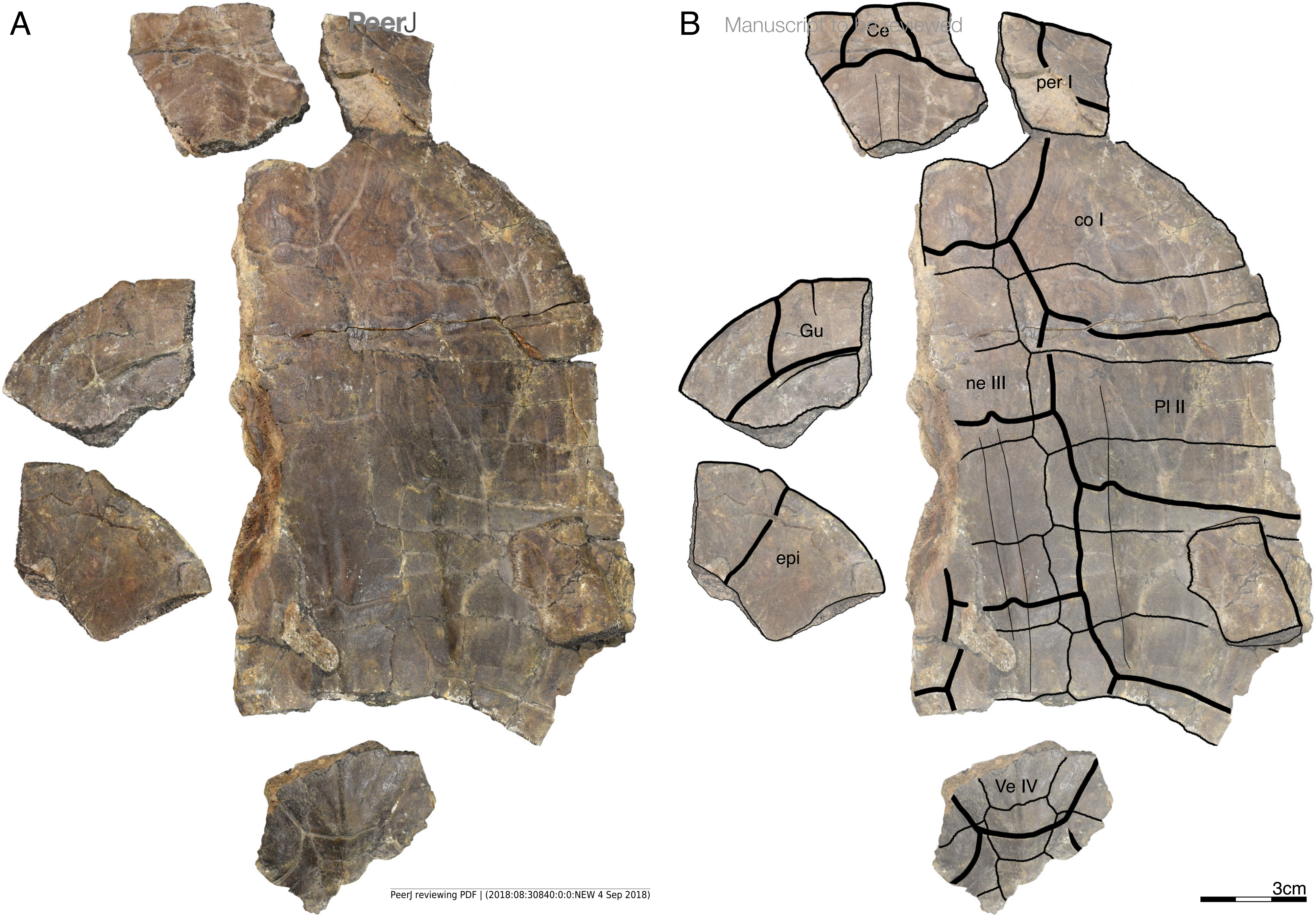
A
B
Ce
per I
co I
Gu
ne III
Pl II
epi
Ve IV
3cm

Figure 7(on next page)

GPIT/RE/09731, *Banhxeochelys trani* gen. et sp. nov., adult, Middle to Late Eocene of Vietnam.

(A) Photograph of carapace. (B) Illustration of carapace. (C) Photograph of plastron. (D) Illustration of plastron. Abbreviations: *Ab*, abdominal scute; *An*, anal scute; *Ce*, cervical scute; *co*, costal; *epi*, epiplastron; *Hu*, humeral scute; *hyo*, hyoplastron; *ne*, neural; *nu*, nuchal; *per*, peripheral; *Pl*, pleural scute; *py*, pygal; *xi*, xiphiplastron.

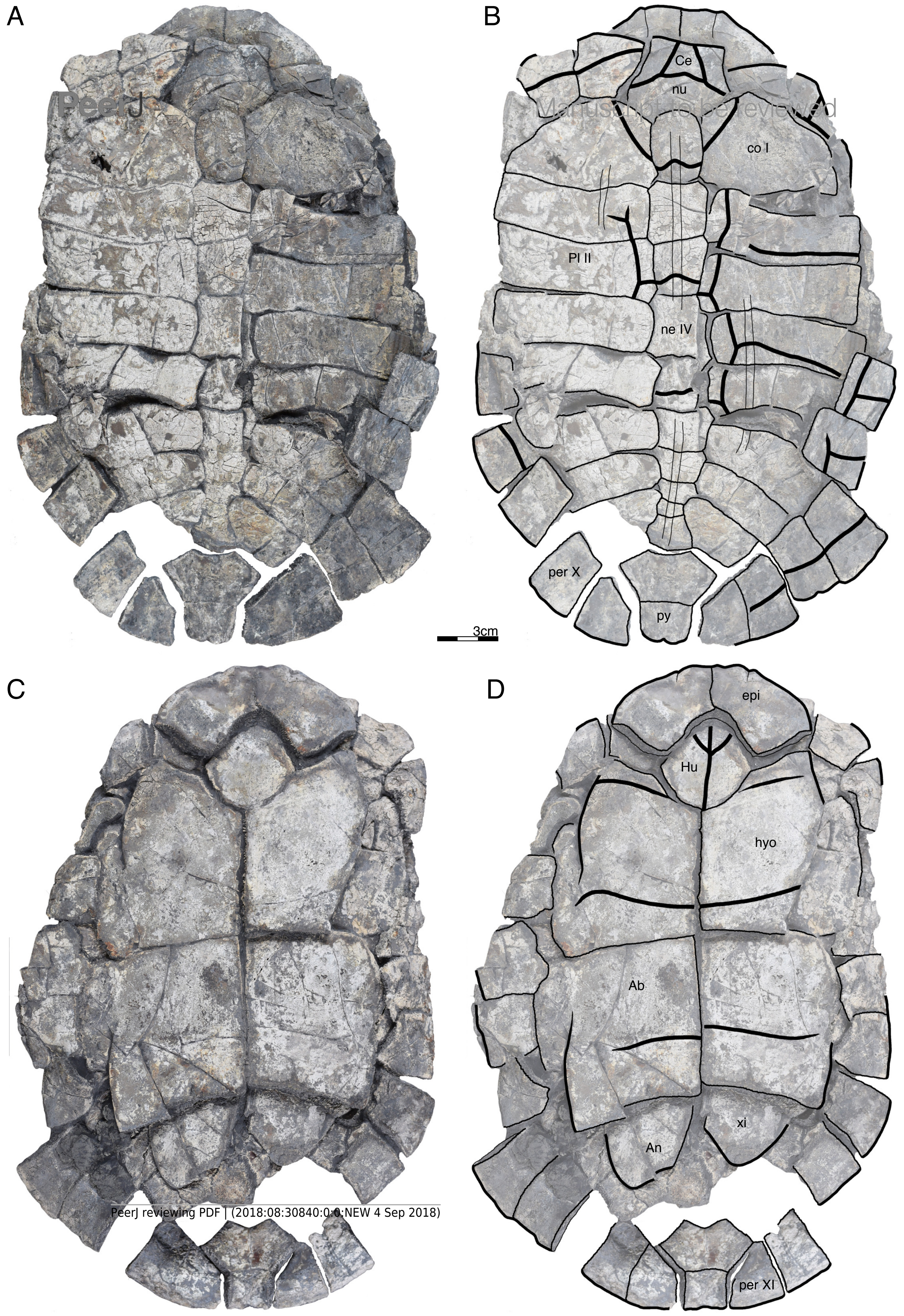

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Figure 8(on next page)

GPIT/RE/09732, *Banhxeochelys trani* gen. et sp. nov., adult, Middle to Late Eocene of Vietnam.

(A) Photograph of carapace. (B) Illustration of carapace. (C) Photograph of plastron. (D) Illustration of plastron. Abbreviations: *co*, costal; *epi*, epiplastron; *Hu*, humeral scute; *hypo*, hypoplastron; *ne*, neural; *nu*, nuchal; *Pl*, pleural scute; *Ve*, vertebral scute; *xi*, xiphiplastron.


A
B
epi
nu
co I
Pl II
ne IV
co V
Ve IV
3cm
C
D
epi
Hu
hypo
xi

Figure 9(on next page)

GPIT/RE/09738, *Banhxeochelys trani* gen. et sp. nov., adult, Middle to Late Eocene of Vietnam.

(A) Photograph of carapace. (B) Illustration of carapace. (C) Photograph of plastron. (D) Illustration of plastron. Abbreviations: *co*, costal; *ent*, entoplastron; *epi*, epiplastron; *Fe*, femoral scute; *Gu*, gular scute; *Ma*, marginal scute; *ne*, neural; *nu*, nuchal; *Pe*, pectoral scute; *per*, peripheral; *Pl*, pleural scute; *Ve*, vertebral scute; *sp*, suprapygal; *xi*, xiphiplastron.

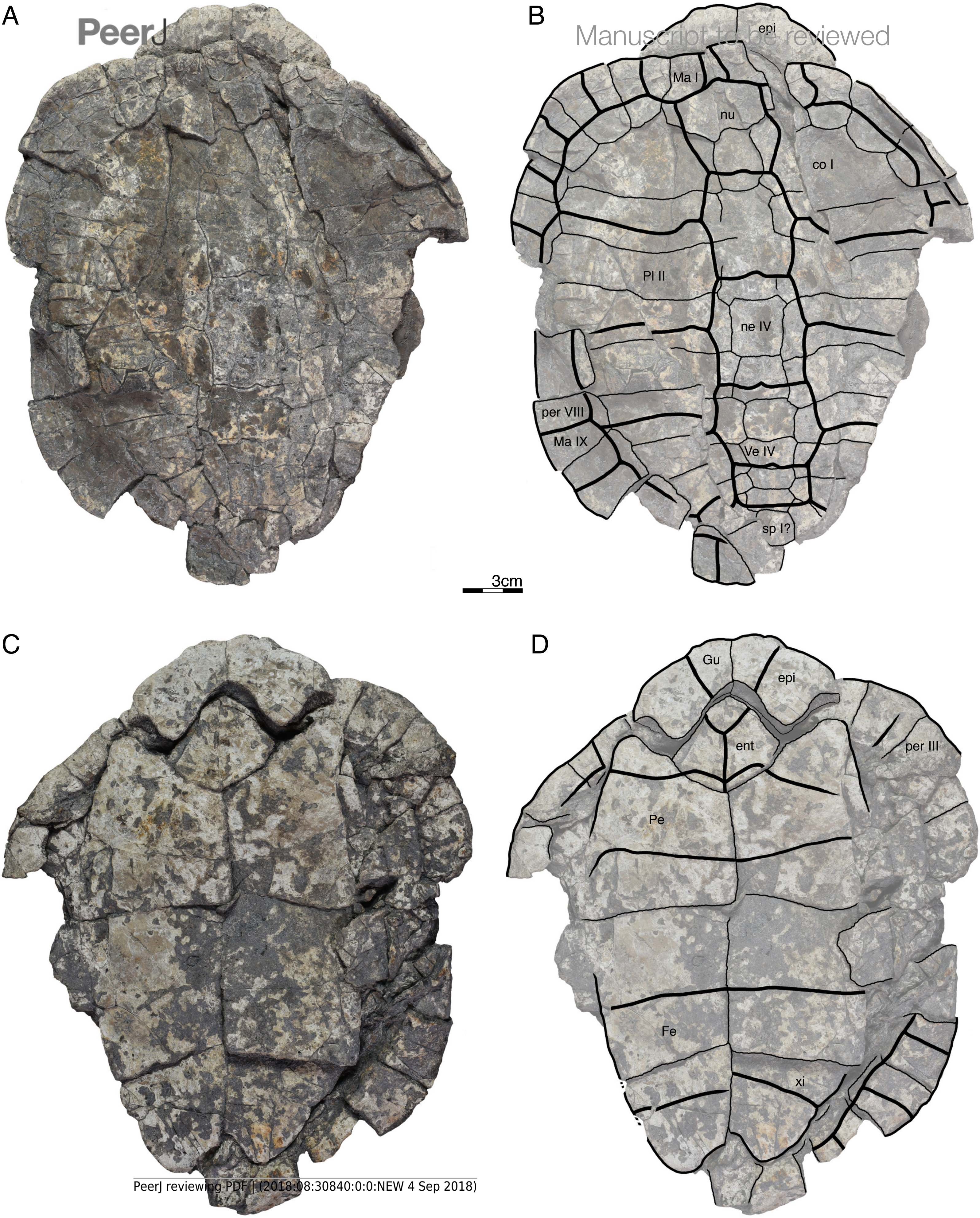
A
B
epi
Ma I
nu
co I
Pl II
ne IV
per VIII
Ma IX
Ve IV
sp I?
3cm
C
D
Gu
epi
ent
per III
Pe
Fe
xi

Figure 10(on next page)

GPIT/RE/09759, *Banhxeochelys trani* gen. et sp. nov., juvenile, Middle to Late Eocene of Vietnam.

(A) Photograph of carapace. (B) Illustration of carapace. (C) Photograph of plastron. (D) Illustration of plastron. Abbreviations: *Hu*, humeral scute; *hyo*, hyoplastron; *Ma*, marginal scute; *ne*, neural; *nu*, nuchal; *per*, peripheral; *Pl*, pleural scute; *spy*, suprapygal; *xi*, xiphiplastron.

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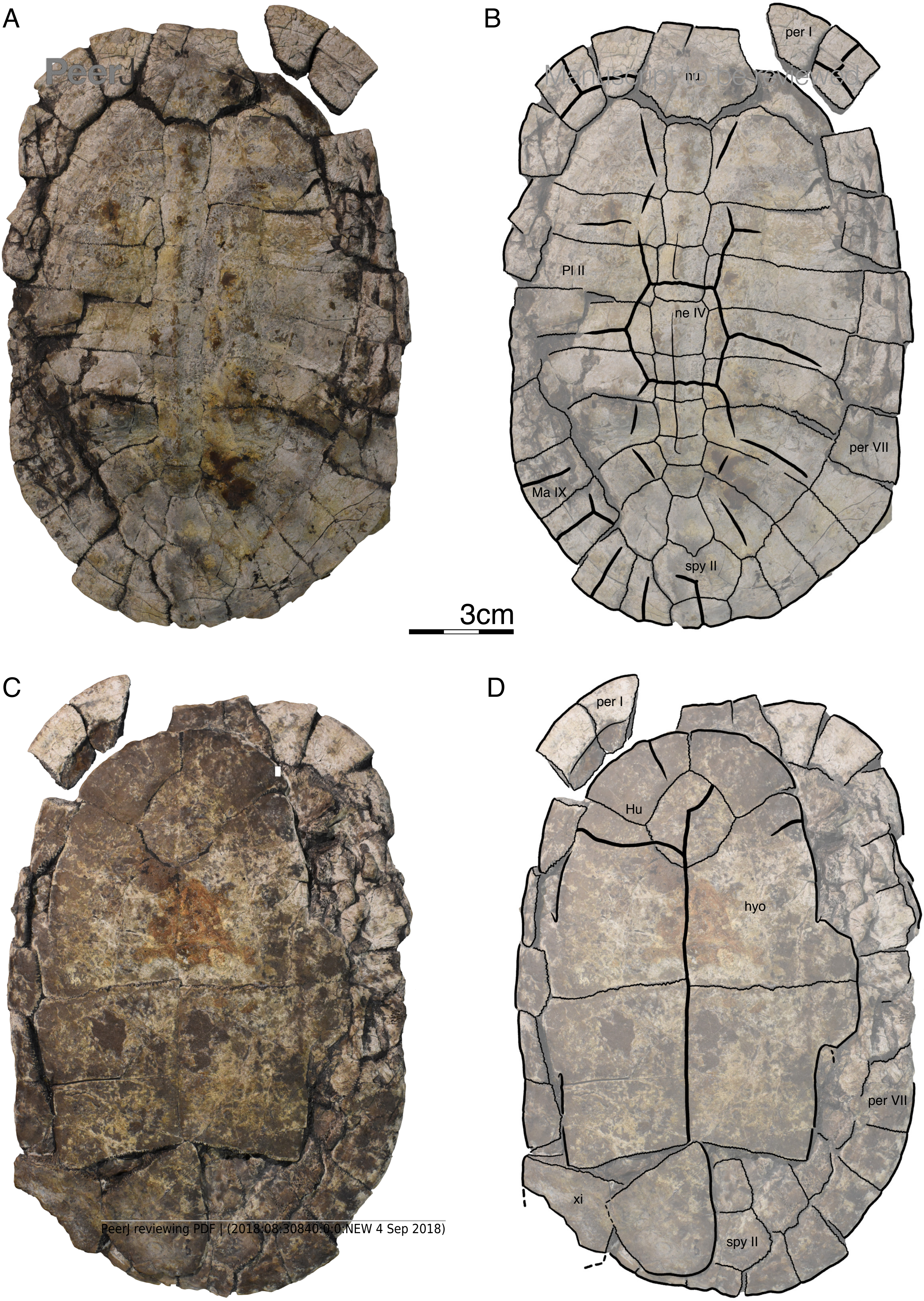

Figure 11(on next page)

GPIT/RE/09743, *Banhxeochelys trani* gen. et sp. nov., juvenile, Middle to Late Eocene of Vietnam.

(A) Photograph of carapace. (B) Illustration of carapace. (C) Photograph of plastron. (D) Illustration of plastron. Abbreviations: *An*, anal scute; *co*, costal; *ent*, entoplastron; *epi*, epiplastron; *Hu*, humeral scute; *hyo*, hyoplastron; *ne*, neural; *nu*, nuchal; *per*, peripheral; *Ve*, vertebral scute; *xi*, xiphiplastron.

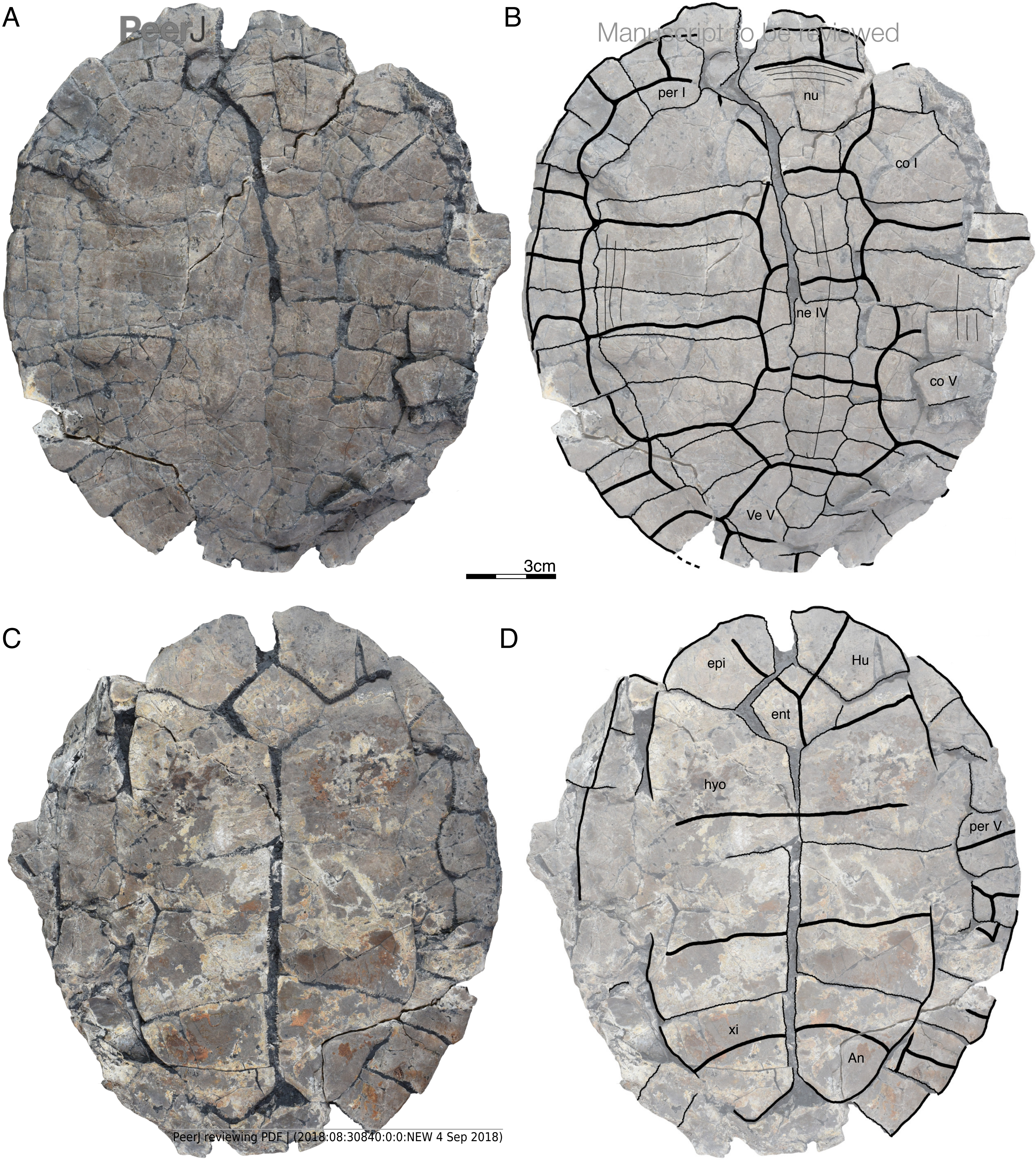
A
B
per I
nu
co I
ne IV
co V
Ve V
3cm
C
D
epi
Hu
ent
hyo
per V
xi
An

Figure 12(on next page)

Median length of the hypoplastron (HypoML) in a sample of 18 specimens of *Banhxeochelys trani*.

The trend in the measurements show the presence of three size groups. Adults have a hypoplastron with 70mm in length or more. Subadults have an average HypoML of 60mm. Juveniles have a hypoplastron median length average of 40mm.

Hypoplastron median length (mm)

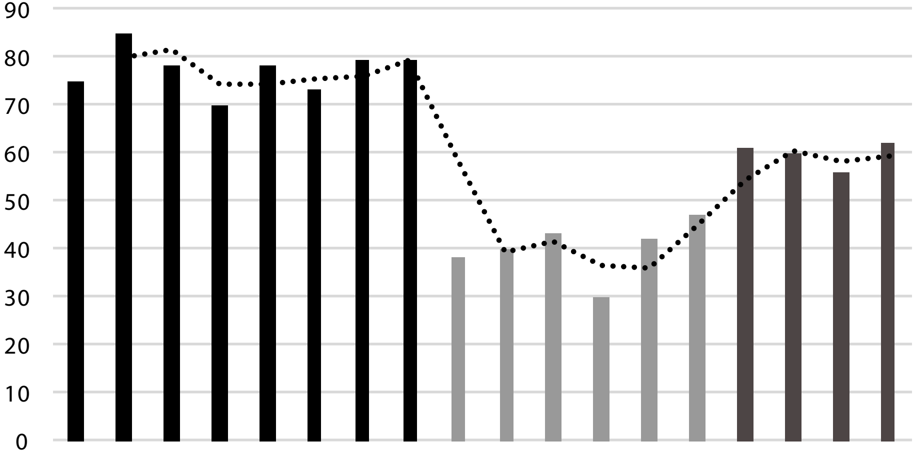

Figure 13(on next page)

Strict consensus of 760375 most parsimonious trees including all extant and fossil species on our matrix.

Fossil species are shown in bold. Major extant clades of Geoemydidae retrieved as monophyletic are marked in colors.

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Manuscript to be reviewed

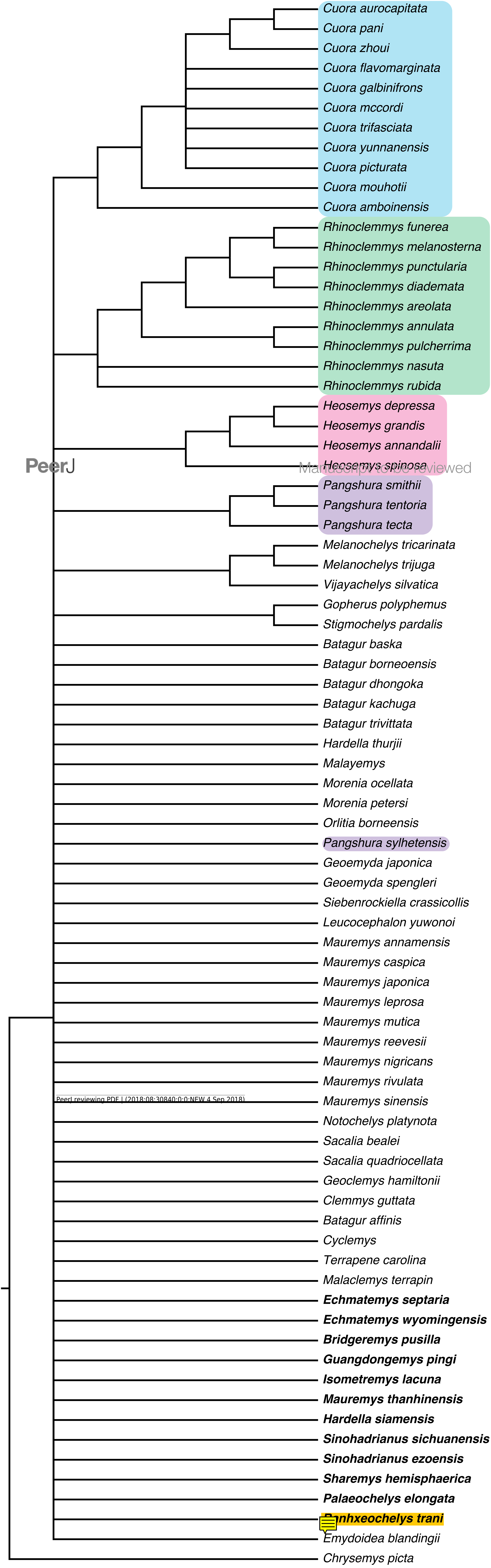


Figure 14(on next page)

Strict consensus of 760375 MPTs after pruning all extinct species with exception of *Guangdongemys pingi* and *Banhxeochelys trani*.

Major extant clades of Geoemydidae retrieved as monophyletic are marked in colors.

Banhxeochelys trani is retrieved at the base of ingroup, Pan-Testuguria.

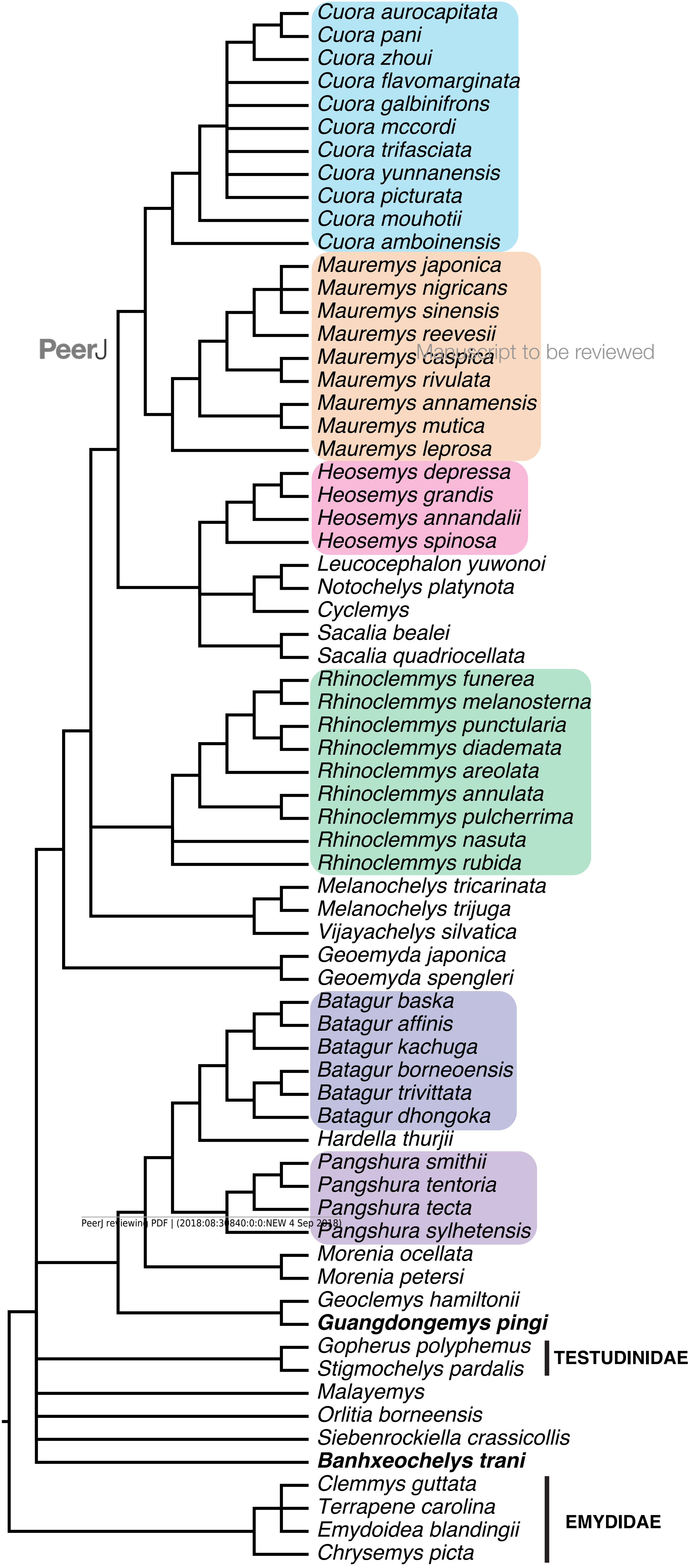

Cuora aurocapitata
Cuora pani
Cuora zhoui
Cuora flavomarginata
Cuora galbinifrons
Cuora mccordi
Cuora trifasciata
Cuora yunnanensis
Cuora picturata
Cuora mouhotii
Cuora amboinensis
Mauremys japonica
Mauremys nigricans
Mauremys sinensis
Mauremys reevesii
Mauremys caspica
Mauremys rivulata
Mauremys annamensis
Mauremys mutica
Mauremys leprosa
Heosemys depressa
Heosemys grandis
Heosemys annandalii
Heosemys spinosa
Leucocephalon yuwonoi
Notochelys platynota
Cyclemys
Sacalia bealei
Sacalia quadriocellata
Rhinoclemmys funerea
Rhinoclemmys melanosterna
Rhinoclemmys punctularia
Rhinoclemmys diademata
Rhinoclemmys areolata
Rhinoclemmys annulata
Rhinoclemmys pulcherrima
Rhinoclemmys nasuta
Rhinoclemmys rubida
Melanochelys tricarinata
Melanochelys trijuga
Vijayachelys silvatica
Geoemyda japonica
Geoemyda spengleri
Batagur baska
Batagur affinis
Batagur kachuga
Batagur borneoensis
Batagur trivittata
Batagur dhongoka
Hardella thurjii
Pangshura smithii
Pangshura tentoria
Pangshura tecta
Pangshura sylhetensis
Morenia ocellata
Morenia petersi
Geoclemys hamiltonii
Guangdongemys pingi
Gopherus polyphemus
Stigmochelys pardalis
TESTUDINIDAE
Malayemys
Orlitia borneensis
Siebenrockiella crassicollis
Banhxeochelys trani
Clemmys guttata
Terrapene carolina
Emydoidea blandingii
Chrysemys picta
EMYDIDAE

Figure 15(on next page)

Summary of the individual position of each fossil species in the strict consensus of 760375 MPTs, keeping only one fossil species at a time.

This figure is based on the consensi from Appendix S4. Clades were reduced to genus name to minimize differences between consensi. *Sharemys hemisphaerica* and the species of *Sinohadrianus* are omitted here, as their consensus was not in agreement with that from other species.

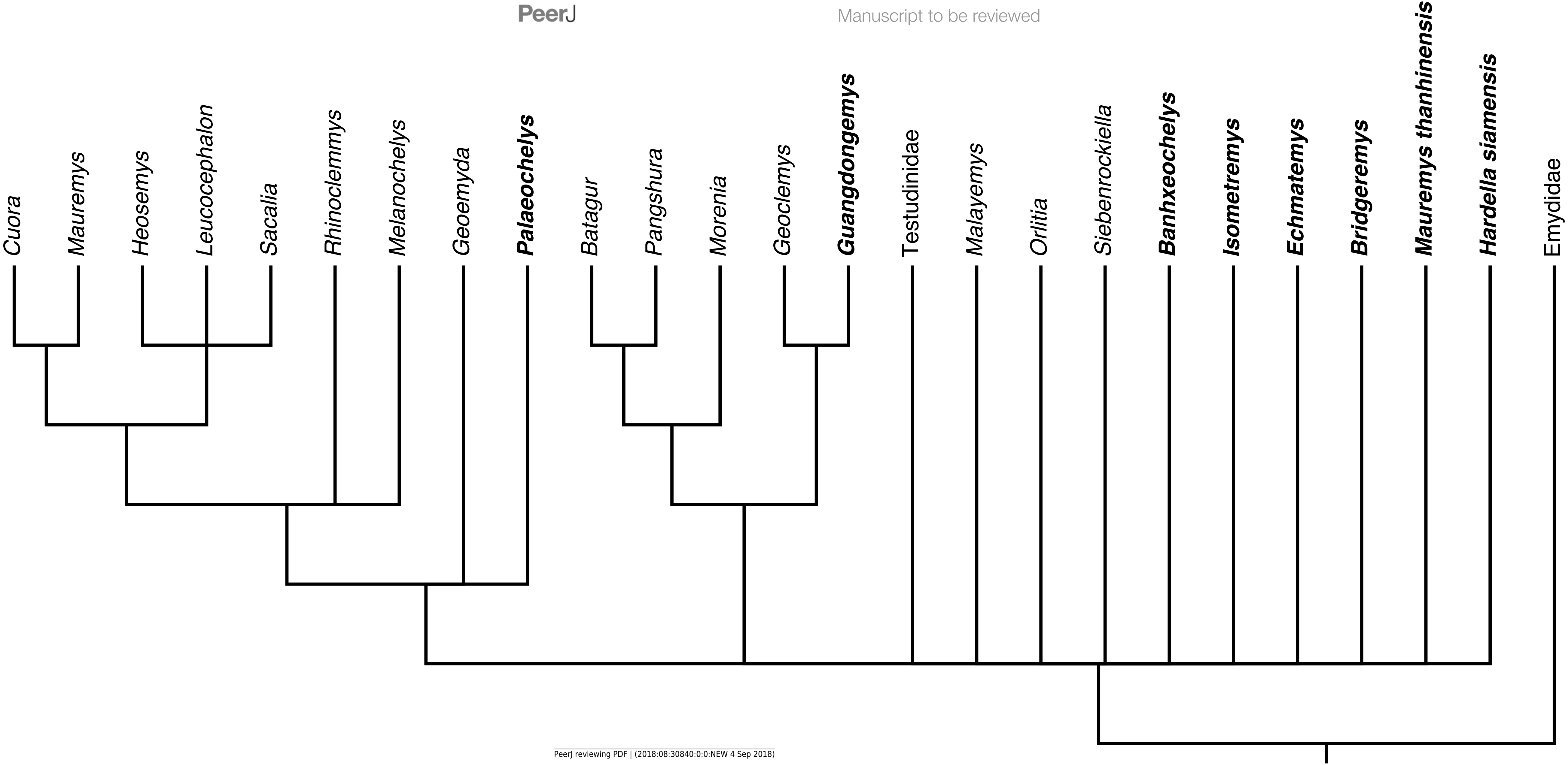
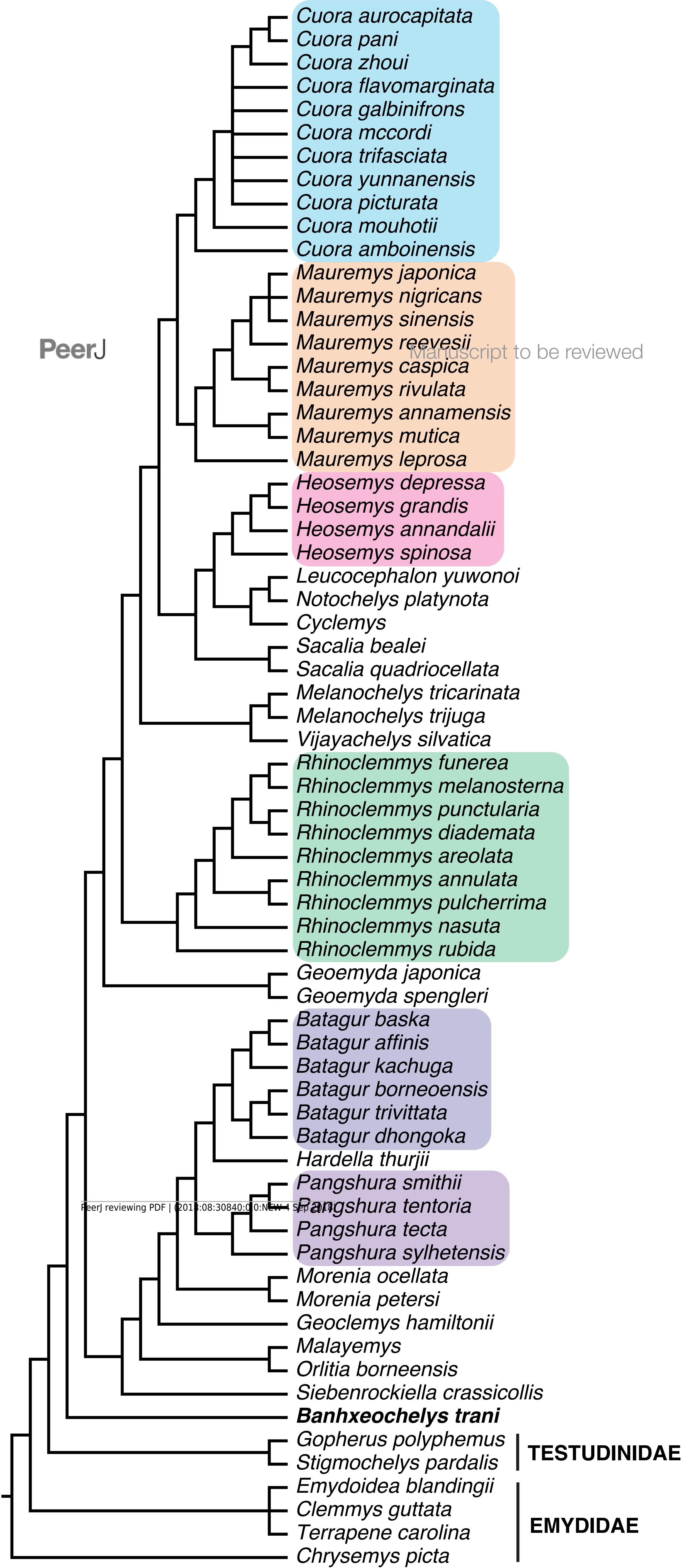

Cuora
Mauremys
Heosemys
Leucocephalon
Sacalia
Rhinoclemmys
Melanochelys
Geoemyda
Palaeochelys
Batagur
Pangshura
Morenia
Geoclemys
Guangdongemys
Testudinidae
Malayemys
Orlitia
Siebenrockiella
Banhxeochelys
Isometremys
Echmatemys
Bridgeremys
Mauremys thanhinensis
Hardella siamensis
Emydidae

Figure 16(on next page)

Strict consensus of 8 most parsimonious trees resulting from analysis that includes *Banhxeochelys trani* as the only active fossil species.

This phylogenetic analysis followed the same parameters as the one for Figure 13. *Banhxeochelys trani* is retrieved as sister to all extant geoemydid species. Major extant clades of Geoemydidae retrieved as monophyletic are marked in colors.


Cuora aurocapitata
Cuora pani
Cuora zhoui
Cuora flavomarginata
Cuora galbinifrons
Cuora mccordi
Cuora trifasciata
Cuora yunnanensis
Cuora picturata
Cuora mouhotii
Cuora amboinensis
Mauremys japonica
Mauremys nigricans
Mauremys sinensis
Mauremys reevesii
Mauremys caspica
Mauremys rivulata
Mauremys annamensis
Mauremys mutica
Mauremys leprosa
Heosemys depressa
Heosemys grandis
Heosemys annandalii
Heosemys spinosa
Leucocephalon yuwonoi
Notochelys platynota
Cyclemys
Sacalia bealei
Sacalia quadriocellata
Melanochelys tricarinata
Melanochelys trijuga
Vijayachelys silvatica
Rhinoclemmys funerea
Rhinoclemmys melanosterna
Rhinoclemmys punctularia
Rhinoclemmys diademata
Rhinoclemmys areolata
Rhinoclemmys annulata
Rhinoclemmys pulcherrima
Rhinoclemmys nasuta
Rhinoclemmys rubida
Geoemyda japonica
Geoemyda spengleri
Batagur baska
Batagur affinis
Batagur kachuga
Batagur borneoensis
Batagur trivittata
Batagur dhongoka
Hardella thurjii
Pangshura smithii
Pangshura tentoria
Pangshura tecta
Pangshura sylhetensis
Morenia ocellata
Morenia petersi
Geoclemys hamiltonii
Malayemys
Orlitia borneensis
Siebenrockiella crassicollis
Banhxeochelys trani
Gopherus polyphemus
Stigmochelys pardalis
TESTUDINIDAE
Emydoidea blandingii
Clemmys guttata
Terrapene carolina
Chrysemys picta
EMYDIDAE